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HETEROSIS

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Geneticists have studied heterosis ever since the rediscovery of Mendelism and are doing so in ever increasing numbers as a result of the success of the hybrid maize industry. The whole subject was reviewed by distinguished workers in every branch of the field at a recent conference organized by Iowa State College. The proceedings of the conference have been published under the title "Heterosis" (Gowen, 1952). It would be superfluous to add another article to those already published in "Heterosis" if it were not for the recent suggestive work on the biochemical genetics of microorganisms. Reference to this work was made by speakers at the conference but, since the implications of the work are not as generally understood as some of the more traditional explanations of heterosis, and as no actual scheme incorporating this new knowledge was put forward at the conference, a possible scheme is put forward here and made the opportunity of summarizing briefly some of the other aspects of the subject discussed at the conference.

THE DOMINANCE THEORY

The explanations of heterosis put forward in the past are not mutually exclusive and there can be little doubt that more than one of the causes suggested are usually operating at the same time. One of the earliest suggestions was made by Jones (1917). It will be referred to as the dominance theory of heterosis. It revolves in various forms round the idea that, if favorable genes are dominant, two populations are very unlikely to have exactly the same set, and so a cross between two lines will produce an F_1 which combines the virtues of both lines. The combinations will not usually reappear in F_2. It is true that in theory one might be able to extract a pure breeding strain from the F_2 equivalent in performance to the F_1. But the practical difficulties of securing the right recombinations might be insuperable if the number of gene differences between the lines were large and if some of the genes were linked. In recent years Mather has discussed the consequences to be expected from the close linkage of genes in two

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different gene systems when one or other of the systems is suddenly submitted to selection. His experiment of selecting for abdominal chaetae in *Drosophila melanogaster*, in which the fate of fertility and various anatomical traits was followed, shows that the effects on the other characters of selecting for chaetae were such as were to be expected if these characters were controlled by systems of linked genes. Selection for one character was accompanied by uncontrollable changes in other characters; fertility was nearly always reduced often to such an extent that the line died out. In lines which survived with reasonable fertility, correlated responses of other kinds made their appearance. This experiment shows that recombinations which would produce as good a pure strain as the F_2 might have to be very extensive and might require the sorting out of many linked genes on the chromosome. An example of this sort of heterosis can be found in dairy cattle. The genes for production of milk with a high fat percentage are to some extent dominant, so that when Friesians, which yield a large volume, are crossed to Jerseys, which yield milk rich in fat, the amount of fat produced by the F_1 is more than that produced by either pure breed. In this type of heterosis the F_1 is superior to anything known before, it exceeds individuals of both populations which went to make the F_1, as it combines the good qualities of both. It does not necessarily refer to any actual or hypothetical random bred population from which, say, both Friesians and Jerseys are derived, or which might arise when the F_1 was interbred.

THE "HARMFUL MUTATION" THEORY

Haldane (1937) and Crow (1948) have demonstrated that so long as genes mutate to forms of lower fitness it must be possible to extract inbred lines from a random breeding population which, when judiciously crossed, will give rise to an F_1 superior in fitness to the random breeding population from which the inbred lines were drawn. The argument runs as follows: The frequency of a gene in a population is increased by mutation, and in the absence of selection or reverse mutation it will eventually reach unity. If the gene is harmful, selection will reduce its frequency. In a population which has reached equilibrium, the number of new genes added by mutation will exactly balance those eliminated by selection. If the gene is completely recessive selection acts on the homozygote only. The frequency of homozygotes increases with the gene frequency and so as the gene frequency increases, more homozygotes are exposed to the action of selection. It is the appearance of these homozygotes which lowers the average fitness of the population. These homozygotes either die before breeding, or have fewer offspring than normal, or have offspring that cannot live, or in some way exhibit inferior vitality to the normal. If they did not appear in the population it would be that much fitter. If inbred lines are taken from the population, lethals and semi-lethals can be eliminated, and, by correct choice of lines to cross, all other harmful recessives can be masked for one generation. This explanation, which I shall refer to as the harmful mutation theory of heterosis, differs from the dominance theory because it does not postulate the production of individuals superior to any in the

random bred population; merely the prevention of the appearance of inferior ones; and because the extent of heterosis is referred to the fitness of the random bred population as a base line. An estimate based on a reasonable guess at mutation rates and gene numbers puts the increase in fitness possible by this means at not more than five per cent. If dominance is incomplete the elimination of the gene is rapid, so that its homozygous effect on the population is reduced or eliminated. Its heterozygous effect will be manifest in the F_1 as much as in the random bred population, so its contribution to heterosis will be negligible.

THE EUHETEROSIS THEORY

A third explanation, which, following Dobzhansky, I shall call euheterosis, is the type which can be exemplified by the balanced lethal stock of the laboratory. The balanced lethal chromosome is familiar to all Drosophila workers. The Cy/Pm stock, for example, has a crossover suppressor in the form of some system of inversions and a lethal gene in the Cy chromosome and its homolog the Pm chromosome, this ensures that all individuals homozygous for the Cy or Pm chromosome die, and perpetuates the heterozygote indefinitely. Dobzhansky has emphasized that similar systems can be evolved by natural selection, and have been so evolved in *Drosophila pseudoobscura*. Drosophila leads an existence which exposes each succeeding generation to a markedly different environment. As the seasons advance, temperature, humidity, and the type of vegetation all change, so that the generation of flies living at the beginning of the season is in a different ecological situation from those following later in the year. Dobzhansky has shown that the third chromosome inversions, of which there may be three or four different kinds in each population, are, if derived from the same population, all at a selective disadvantage in homozygous condition. This ensures the continued survival of all the inversion types in the population, since the larger the number of different types the greater the proportion of heterozygotes. Dobzhansky has also shown that the exact selective value of the different orders, and their heterozygote combinations, changes with temperature. The inversions prevent the gene combinations responsible for the selective advantage from being broken up, and so a mechanism has evolved which enables Drosophila to adapt itself, as a population, to rapid changes in environment. A change of season is accompanied by a change in frequency of preadapted chromosome segments which are preserved in the population by the system of heterozygote superiorities. As pointed out by Dobzhansky in "Heterosis," this evolutionary mechanism is of a different sort from the other types of heterosis. It is comparable to other mechanisms conferring selective advantage on the heterozygote. Most of these depend on some unevenness in the environment, such that one genotype is favored in one, and one in the other situation. As Professor Penrose has pointed out to me, one might also get a balance if an allele had an advantage in one sex but a disadvantage in the other. Such situations are of great interest in evolution but have little bearing on the type of phenomenon usually referred to as heterosis.

THE OVERDOMINANCE THEORY

A fourth explanation was originally put forward by East. According to this theory the heterozygote was of itself better than either homozygote. In East's version it was supposed that the two alleles both did something different in the heterozygote which could thus combine in itself qualities present in the two homozygotes. A good illustration of this sort of gene action is the blood groups of man. An A individual produces only one sort of blood corpuscle, A; the B individual only the type B; the AB individual produces corpuscles which are both A and B. The main criticism of this explanation does not question the practical effect of being heterozygous, but questions the classification of the two genes, A and B in this example, as alleles. It is suggested that they are closely linked genes and that this explanation, which I shall call the overdominance theory, is a version of the dominance theory with extremely tight linkage. The criticism is based on the work by Lewis, amongst others, with position effect of the Star-asteroid type. In this type of position effect it has been found that the heterozygote, with the two mutant forms in coupling, is normal with respect to the recessive member of the pair, but that when the heterozygotes are in repulsion the recessive is no longer recessive; the genes behave as alleles in that the recessive is manifested in the heterozygote. The suggestion is that genes are often associated in a process in which one gene uses the product of another, transforms it, and passes the transformed product on to the next gene and so on. When such an association exists it is of advantage for the genes to be next to one another on the chromosome. If the chromosome does not form many chiasmata at the point where the genes are located this will result in such tight linkage that crossingover becomes indistinguishable from mutation. The position effect arises because with two normal genes side by side on one chromosome, the process in which the genes are engaged can proceed, but when the chain is broken in both chromosomes the synthesis is interfered with in both, and so the effect of the recessive is noticed. The ideas behind this explanation of position effect are supported by cases in which genes acting as successive steps of a synthesis are closely linked. The overdominance theory differs from the dominance, first by postulating an independently recognizable action of both genes in a heterozygote, and second because the advantage of the F_1 is theoretically unfixable. In this theory the advantages of two pure breeding types are combined, but the heterozygote would be preserved in a random mating population, so that a polymorphic population would result.

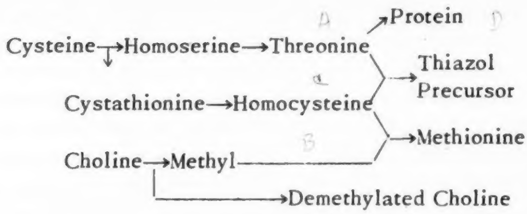
PHYSIOLOGICAL BALANCE THEORY

The other version of the overdominance theory, which I shall call the physiological balance theory, supposes that the two homozygous expressions of a pair of alleles are less suitable to optimum development of the organism than the intermediate one. A model for this explanation comes from the work of Emerson, (1948) also reported in "Heterosis," on the sulphonamide requiring strain of Neurospora. In this strain normal growth

will not take place unless sulphonamide is present. The reason is supposed to be that the p-aminobenzoic acid produced by the strain inhibits normal growth. The sulphonamide slows down the production of p-aminobenzoic acid. Through balance of nuclear proportions in a heterokarion between a strain requiring sulphonamide and one requiring both sulphonamide and p-aminobenzoic acid, the right balance is struck between producing too much or too little p-aminobenzoic acid. The homokariotic producer of p-aminobenzoic acid produces too much, whereas the homokariotic non-producer cannot grow without p-aminobenzoic acid supplement; the heterokariotic individual, however, can grow without either sulphonamide or p-aminobenzoic acid, although homokariotic for the sulphonamide requiring gene. It is the possible ramifications of this sort of balance which gave rise to this article.

As Robbins has suggested (1952), a study of the physiology and biochemistry behind hybrid vigor is likely to bring increased understanding of the genetic mechanism also. It is becoming increasingly common to find that genes which bring about nutritional requirements in micro-organisms do so by upsetting some balance. The case already cited is one in which the mutant cannot manufacture some essential growth substance in the presence of an excess of p-aminobenzoic acid. This is a relatively simple example which can be cited as typical of many. It is not always clear whether the fault lies with the gene responsible for the suppressed synthesis or with the gene controlling the suppressor. A particularly interesting case from this point of view was worked out by Wagner and Haddox. A strain normally deficient in pantothenic acid was found to produce enough for growth when aerated, showing that the capacity to make pantothenic acid was there in the deficient organism, given the right conditions. This suggested a suppression of the production of pantothenic acid, and a search for possible suppressors revealed that in normal organisms addition of tryptophane (as well as some other substances) to the medium reduces the manufacture of pantothenic acid. If a strain were deficient in pantothenic acid because it was sensitive to tryptophane, then, when combined with tryptophane deficiency, it might not show so marked a lack of pantothenic acid. Wagner and Haddox crossed two strains, one of which was deficient in pantothenic acid and the other in tryptophane, and recovered a strain which proved to carry pantothenicless but would grow on basal medium. It could not be proved, however, that it also carried tryptophaneless, though it may have done so. The suggestion that pantothenic acid production in the pantothenicless strain was suppressed by tryptophane thus received some support. What is perhaps most significant in this work is that in the normal Neurospora, production of pantothenic acid could be suppressed by addition of tryptophane. Suppression of one metabolite by another is therefore a characteristic of normal, as well as mutant, Neurospora, although more dramatic in the mutant forms.

Doudney and Wagner report a more complicated case of interaction between substances in a strain, which, while normal in growth at 35°C., is suppressed by addition of threonine. The authors suggest the following model:



Homocysteine is required for the manufacture of methionine and in combination with threonine for other essential growth substances. An excess of threonine starves the methionine producing reaction of homocysteine. The excess can be counteracted either by providing methionine, which acts directly to relieve the shortage of methionine created by excess threonine, or by giving homocysteine in sufficient quantities for both the threonine reaction in excess, and the production of methionine. An excess of choline, on the other hand, while resulting in production of methionine, starves the threonine reaction of homocysteine. Optimum growth is only produced when the production of threonine choline and homocysteine are properly balanced.

A PHYSIOLOGICAL MECHANISM FOR HETEROSIS

This interaction can be used as a model for a mechanism which would result in heterosis. Suppose we have a common precursor C, such as homocysteine, being utilized by two substances, A and B, such as threonine and choline, to make D and E. If too much A is present B is starved of C, and if too much B, A is starved of C. If the rate of both reactions is controlled by a pair of additive alleles *Aa* and *Bb*, such that *AA* will keep pace with *BB*, *aa* with *bb*, and *aA* with *bB*, then *AABB*, *aabb*, and *aAbB* will all be in balance, but any other combination will result in a deficiency of A or B. E and D may also be required in some fixed amount. We may suppose that the optimum production of D is given by a gene combination *CCaa*, or *CcAa*; and an optimum of E by *ccBB*, or *CcBb*; so that *AaBbCc* will give the best results. We may further suppose that *AABBcc* or *aabbCC* will not be far short of optimum. The important point about this model is that it can be shown, by giving arbitrary selective values to the combinations *AABBcc*, *aabbCC*, and *AaBbCc*, and lower ones to any other combination, that a random breeding population would be unstable if all three alleles were heterozygous. As soon as any of the alleles strayed far from a frequency of 0.5 the system would move steadily towards fixation, either of *AABBcc* or *aabbCC*, as pointed out by Sewall Wright. Even with high selective values of the triple heterozygote fixation results, provided the two homozygotes have some selective value also.

If mating is at random and the two alleles of all three genes are at a frequency of .5 there will be no change in gene frequency no matter what the fitnesses of genotypes so long as they are symmetrical. The triple heterozygote gives rise to both alleles of all three genes in equal numbers

and the increase of *A*, *B* and *c* alleles brought about by the extra fitness of the *AABBcc* genotype is exactly balanced by the increase in *a*, *b* and *C* brought about by the extra fitness of the *aabbCC* genotype. If A is increased in frequency, the first effect will be an increase in *AABBcc* genotypes, and a corresponding decrease in *aabbCC*. The frequency of *AaBbCc* will be reduced also, as it is at a maximum when the alleles all have a frequency of .5. This is obvious as $p(1-p)$ must be maximum when $p = 0.5$ since $.5 \times .5 = .25$ is greater than $(.5 + h) \times (.5 - h) = .25 - h^2$. An increase in the frequency of A will thus tend to increase *AABBcc* and decrease *aabbCC* and to reduce the influence of *AaBbCc* relative to the homozygous types. Now as *AABBcc* no longer equals *aabbCC* in frequency, the tendency of the former to increase A, B and c is no longer compensated by the tendency of *aabbCC* to increase a, b and C; since *AABBcc* is more frequent than *aabbCC* but has the same fitness, the product of frequency and fitness is no longer equal. As *AaBbCc* has a fitness greater than any other genotype, and is therefore producing a disproportionate number of the gametes of the population, there will be a tendency for all alleles with a frequency of less than 0.5 to be raised to 0.5 and all those with frequencies greater than 0.5 to be reduced to 0.5, as this genotype is producing gametes of both kinds of allele in equal numbers. The actual movement of gene frequency will result from the interaction of the tendency of the homozygotes to increase the frequency of *A*, once it is greater than 0.5, and the triple heterozygote to keep it at 0.5. If the fitness of the heterozygote is large relative to the other genotypes it will succeed in keeping frequencies to 0.5, unless the shift of gene frequency is very great. The larger the difference in fitness, the larger the frequency of *A* must be before it runs to fixation. Genotypes other than those mentioned will exert similar pressures on gene frequency but will be less important as they have a lower fitness.

In figure 1 curves have been drawn which show the rate of change of the gene frequency of *A* under different conditions. The solid lines show what happens when all genotypes except *AABBcc*, *AaBbCc* and *aabbCC* have a fitness 0. In all curves *AaBbCc* has fitness 4, the other two genotypes have fitness 3 in curve 1, 2 in curve 2, and 1 in curve 3. The vertical axis shows the change in the frequency of *A* in a generation, the horizontal axis shows the frequency of *A*. The calculations have all been made when the population is in balance, in this case when $p = q = 1 - r$ where p is the frequency of *A*, q the frequency of *B*, and r the frequency of *C*. The broken lines show what happens when all genotypes have a fitness of more than zero. The actual fitnesses are given in the table. As before, fitnesses have been chosen so that after one generation of random mating $p = q = 1 - r$ and change of frequency is calculated from this point. It is not necessary for p to $= q = 1 - r$ for gene frequencies to move, but the calculations are much shorter if this condition holds as the balanced position is automatically given and need not be calculated.

It can be seen from the solid curves that even when the triple heterozygote has four times the fitness of the homozygotes, A will run to fixa-

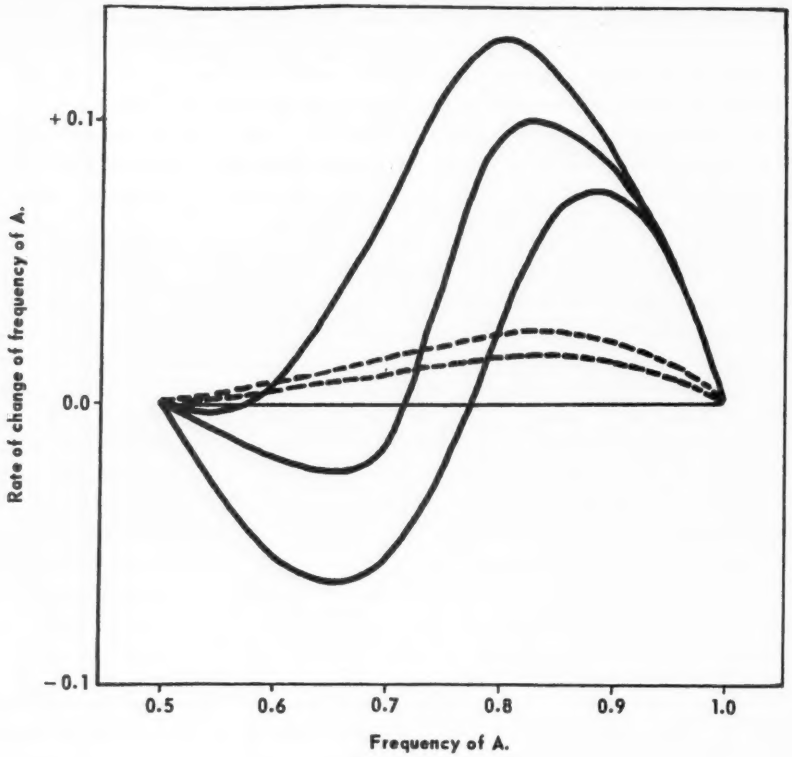


FIGURE 1.

TABLE 1

Genotypes	Fitness Curve 4	Curve 5
AABBCC aabbcc *AAbb all types* *AaBBCC Aabbcc* *aaBB all types* *aaBbcc AABbCC*	1	2
AABBCc aabbCc *AABbcc AAbBCc* *AaBBCc AaBBcc* *AaBbCC AaBbcc* *AabbCC AabbCc* *aaBbCC aaBbCc*	2	3
AABBcc aabbCC	3	4
AaBbCc	4	5

tion if it once reaches a high enough frequency. It is perhaps unlikely that the three genes would ever reach frequencies of 0.74, 0.74 and 0.26, or 0.78, 0.78 and 0.22, which they would have to do before *A* would run to fixation, in conditions obtaining for curve 2 and 3. But in curve 1 only minor deviation from .5 will lead to fixation. The dotted lines show that changes are much slower where all genotypes survive, the relative importance of the triple heterozygote and the two homozygotes being less, but that any deviation from 0.5, however small, leads to fixation.

The explanation of heterosis on the physiological balance theory differs from the dominance explanation in that where several gene pairs enter into the picture the optimum type tends to be eliminated from a random breeding population through fixation of other types, and also because the optimum type could, in theory at least, be fixed according to the dominance theory, but not according to the physiological balance theory. The physiological balance theory differs from the overdominance and harmful mutation theory in that according to these, the frequency of already existing advantageous genotypes is raised to a maximum—nothing new is produced—whereas according to the physiological balance theory a new genotype is set up, which cannot survive long in a random bred population. Unlike the overdominance theory, according to which heterosis will be expected to lead to polymorphism, the physiological balance theory leads one to suppose that populations will always tend to run to fixation of one genotype or another, despite the selective advantage of the triple heterozygote, and we may therefore expect that populations which have been separated by some scores of generations will have run to near fixation, and may have done so in opposite directions; that is, one population may have fixed *AABBcc*, and the other *aabbCC*, in which case a cross will give hybrid vigor. We thus have a mechanism which, despite the advantage of the heterozygote, will result in homozygous populations capable of exhibiting heterosis on crossing.

In "Heterosis" both Whaley and Robbins emphasize the importance of physiological balance in Neurospora, and point to the fact that experiments with roots of higher plants show that they too require a balance between exactly the same types of substance as are of importance to Neurospora. Robbins, for example, has found that roots of tomatoes which, when crossed, give a hybrid showing heterosis, differ with respect to their response to thiamine, pyridoxine and nicotinamide. In one parent, growth improved if pyridoxine and thiamine were added. The second parent was not improved by thiamine and pyridoxine, but was by addition of nicotinamide. Heterosis, in fact, may well be due to interaction between gene products responsible for growth, and in a sense competing with each other, success being achieved to a large extent by balance, not by absolute rates of reaction.

SUMMARY

Different possible mechanisms which may be responsible for heterosis are summarized as follows:

Heterosis may be due to:

(1) Dominant genes in one parental strain which supplement the action of dominant genes in the other parental strain.
(2) The avoidance in one generation of the occurrence of homozygous deleterious recessives which, in normal populations in equilibrium, are kept at a certain level by the joint action of mutation and selective elimination of homozygotes.
(3) Due to balanced chromosomal mechanisms (eu-heterosis).
(4) Due to the superiority of the heterozygotes at individual loci brought about by the actions of the two alleles which are different and manifest in the heterozygote, as, for example, A and B in human blood groups. The heterozygote goes beyond both homozygotes.
(5) Due to interaction between gene products which are essential growth substances.

The differences between, and possible consequences of, these five explanations of heterosis are briefly discussed. It is pointed out that where the fifth explanation operates with more than two gene pairs concerned, a situation can be set up in which, despite considerable advantage of the heterozygote, the population will nevertheless run to fixation. This type of heterosis will result in pure breeding populations which, when suitably crossed, will exhibit heterosis.

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A THEORY OF GROWTH LIMITATION*

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INTRODUCTION

The first purpose of this paper is to gather together and discuss the evidence concerning a theory of growth limitation. The theory itself was proposed several years ago (Moment, 1946) but subsequent contributions to it have been published piecemeal in various places. The second aim is to consider more fully than heretofore the relationships of such an hypothesis to other theories about growth.

The original considerations out of which the theory arose consisted in a re-investigation of the facts of earthworm growth and regeneration. Consequently, it seems appropriate to begin with a critique of previous theories of growth and regeneration in earthworms in the light of present information.

PREVIOUS IDEAS AND THE TRUE LIMITATION OF EARTHWORM GROWTH

It has been the generally accepted belief that earthworms continue to grow throughout life by the proliferation of new segments at, or just anterior to, the extreme posterior end of the worm (Hyman, 1940). According to this view there is no limitation to the growth of an earthworm except the death of the worm. Only Sun and Pratt (1931) had published views at variance with those accepted by Hyman. They found that earthworms hatch from the egg cocoons with the full adult number of segments, but their work has been challenged by at least one oligochaetologist (Gates, 1949).

However, the conclusion of Sun and Pratt has now been abundantly confirmed by four different methods. Clitellate adults of the common barnyard species, *Eisenia foetida,* were placed in a box of soil, the egg cocoons collected, and the segments of the wormlings counted as they emerged. Such wormlings had, on the average, the same number of segments as adults (Moment, 1950a, 1950b). Secondly, it was found in posterior regeneration from the 50th segment that new segments formed over a period of about 21 days, after which no new segments appeared, though the worms were kept for 60 days (Moment, 1949a).

Furthermore, normal earthworms of this species still in the process of forming additional segments can be seen, but only by cutting open cocoons and observing what might be termed larval stages. And fourthly, individual worms grown in isolation from the time of emergence from the egg cocoon increase many times in size but remain constant in the number of segments (unpublished observations).

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Previous Theories of Earthworm Regeneration. The general view regarding posterior regeneration has been that the more tissue which is cut off from the hind end of a worm, the more will be regenerated (Morgan, 1901, 1906). This view reflected the prevailing theory (Zeleny, 1903, and others) that the amount of regeneration is proportional to the amount of injury.

The evidence on which this view was based is surprisingly meager. In an exhaustive review of posterior regeneration, Gates (1950) found there was a combined total of only 200 cases in the literature prior to 1946 when the survey of 335 cases described below was published. More important, most of the earlier cases were of worms cut anterior to the level of the 25th segment where virtually no posterior regeneration occurs. The 40-odd positive cases amputated at more posterior levels were widely scattered, with only three groups of as many as five cases at any one level. And in these it is impossible to know the actual level of amputation, because Morgan and Michel, who did this work, reported only the number of segments removed, counting from the posterior end. In fact, as shown in the following paragraphs, it would be possible to set up an experiment in which the more segments amputated, the fewer would be regenerated.

When a systematic survey of over 300 cases cut at but five definite levels (immediately posterior to the 40th, 50th, 60th, 70th, and 80th segments) was made (Moment, 1946), several new relationships became clear. As shown in figure 1, (Moment, 1950a) if 180 worms are cut at the level of the 50th segment and assorted into six groups according to the original number of segments possessed, it is found that, on the average, approximately 40 segments are regenerated regardless of the original number. If the number of segments removed determines the amount of regeneration, then each of the six groups should have regenerated successively more and more segments. Such was not the case. Although each of the six groups lost more segments than any of the preceding groups, there was no significant difference in the number of segments regenerated.

It has also been held by Abeloos and Avel (1928), Liebmann (1942), and others that reproductive activity and regeneration are mutually antagonistic in earthworms. However, as indicated by the degree of development of the clitellum (the accepted sign of reproductive condition), there is no correlation between reproductive state and the number of segments regenerated, when worms were cut at the 50th segment (Moment, 1950a, fig. 1).

The same figure illustrates the lack of correlation between the number of segments regenerated and the actual total length in millimeters for four groups of worms ranging in length from 21 to 60 mm but all cut at the level of the 50th segment. On the other hand, *a marked and linear correlation is evident between the level of amputation, in terms of number of segments from the anterior end, and the number of segments regenerated.* Every time the level of amputation is moved ten segments posteriorly, the average number of segments regenerated decreases by ten.

The only other recent theory of regeneration in earthworms is that of Liebmann (1942, 1945). The difficulties of this theory have already been

discussed in detail (Moment, 1946). Briefly, Liebmann proposed that the rate and amount of regeneration are proportional to the amount of nutritive chloragogue tissue present. He found, however, that long pieces of worm regenerated far less, and short pieces far more than would be expected according to such a theory.

THE SELF-PRODUCED INHIBITORY VOLTAGE THEORY OF GROWTH LIMITATION

The facts of regenerative growth in earthworms, on which the self-produced inhibitory voltage theory was originally formulated, can now be restated in the following terms. In the common barnyard earthworm, *Eisenia foetida,* posterior regeneration takes place by the proliferation of new segments only at the extreme posterior tip of the regenerating end. New segments continue to be formed at that point until, on the average, the original old segments plus the regenerated new ones summate to the species mean of approximately 90 segments. Fifty large old ones plus 40 small young ones have the same inhibitory effect at the distal proliferating end zone as do 80 large old segments and only 10 of the small young ones. More precisely, segments 51 through 80 are large old segments in one case, small young ones in the other. Yet these two groups of thirty segments, so different in size and in age, are in some manner the equivalent in inhibitory value at the distal end of the worm.

These observations led to the conclusion that "whatever may be the force or influence that finally stops the formation of new segments out at the end of the worm, it must fulfill certain conditions." (Moment, 1946) (1) It must be independent of the size of the unit producing it. (2) It must be closely dependent on the number of those units in linear series. (3) Its action must attain its full force at the very end of the series. The only well-known force that fulfills all three of the requirements is the e. m. f. of a series of galvanic cells.

At the same time, as has been demonstrated by a series of investigators, (see below) electrical potentials do in fact inhibit growth. Consequently, it seems reasonable to suppose that in their linear dimensions, animals like earthworms continue to grow by the proliferation of voltage-producing units until, by the summation of these units, a critical inhibitory voltage is built up. The proliferation of these units, whether they are cells or segments, occurs in the distal growing region, and it is in this region that the inhibitory voltage reaches the threshold value which finally blocks proliferation. It is important to note that subsequent growth both of the segments and of the cells of which they are composed is extremely great, but that this later growth is by enlargement of existing structures, and not by proliferation.

ELECTRICAL EVIDENCE CONCERNING A SELF-PRODUCED INHIBITORY VOLTAGE THEORY

It is now half a century since Mathews (1903) discovered that coelenterates and teleosts are electrically polarized, and suggested that such elec-

trical differences between different regions of an organism, "like any constant current applied from the outside, polarize the protoplasm of the cells in a definite way, causing alterations in their metabolism." It was in 1921 that Lund first proved that applied electrical potentials would, in fact, reverse the polarity of an animal. Since then many of the details have been worked out by Lund and his associates as well as by Barth (1934). Lund (1921–1947) has described the polar electrical characteristics of plants and coelenterates, and has argued that the "electric field acts as a directive force" in "correlating morphogenetic processes and polar and vector properties of cell and tissue functions."

Beginning somewhat later, Burr (1937, 1947) and his associates have continued the investigation of this problem and have shown that many, and perhaps all, animals and plants possess an electrical polarity. More important, they have found that in the salamander Amblystoma and in mice the potential measurable between the ends of the animal increases during growth to an asymptote. This discovery seems to have become lost in a large number of other electrical determinations on adult plants and animals, and has not been intimately correlated with anatomical development. In any case, Burr and his associates, like Lund, stated their conclusions in extremely general terms. In fact, Burr (1947), has merely said, "the data suggest that these electrical attributes are of such widespread occurrence that, in all probability, they are of more fundamental significance than has been generally assumed. It seemed worthwhile, therefore, to study living organisms from the point of view that the electrical manifestations are a sign of a fundamental electrodynamic field."

The most important objection that has been raised against the view that bioelectrical potentials influence development has been well expressed by Barth (1940).

> The fact that organisms show patterns of electrical differences in potential is not in itself any evidence that these potentials have anything to do with the development of this pattern. Indeed, it is unthinkable that the stem of a hydroid, with its cells containing electrolytes and having semi-permeable membranes, would not show electrical differences in potential. And further, since the cells do not form a homogeneous system, it follows that there must be some sort of pattern formed by these potential differences. Then, too, it is impossible to conceive of any living system which would not be affected by passing an electric current through it. Therefore these two phenomena are merely necessary results of the organization of any living system, and their existence is not in any way significant to the problem of dominance.

But Barth very sensibly ends this paper by pointing out that,

> Dominance, or the inhibitory effect of a regenerating region, can be explained either on the basis of electrical differences in potential which produce chemical inhibition, or as the competition of regions of the stem for hypothetical substances circulating in the stem... both [theories] should be subjects for investigations.

The mass of evidence against the theories that nutritive competition is the controlling factor will be discussed later. The view that bioelectric potentials are "merely" necessary concomitants of cellular organization and activity and therefore "not in any way significant" to the problems of

growth seems an extreme view and difficult to follow. In fact it appears on the face of it to be self-contradictory, like attempting to argue that although alcohol added to the medium in which yeast cells are growing tends to inhibit the growth of the yeast, the alcohol which the yeast itself produces will be without effect on the yeast cells, a statement that of course is contrary to the known facts.

CORRELATED ANATOMICAL AND BIO-ELECTRICAL PHENOMENA

If the preceding theory of a self-produced inhibitory voltage is valid, it should follow: (1) that worms (and other animals) should have a fixed electrical polarity, (2) that large and small worms with a similar number of segments (or cells?) should possess similar voltages end to end, (3) that during development and regeneration the e. m. f. between the ends of the worm should gradually increase to an asymptote, and (4) that proliferative growth in a terminal growing zone should slow to an asymptote concomitantly. If these conditions are fulfilled, the theory is not thereby proven, but is rendered more probable. If they do not hold, then the theory becomes untenable.

In regard to the first condition, Watanabé (1928) found a fixed electrical polarity with the posterior end positive to the anterior in an oriental earthworm. A similar polarity has also been found to be characteristic of the American species tested, *Eisenia foetida, Lumbricus terrestris,* and *Octolasium lacteum* (Moment, 1950b). Burr and Hovland (1937) have found that a number of vertebrates possess such an electrical polarity with the posterior end positive to the anterior. Mathews, Lund, and Barth (loc. cit.) have firmly established the fact of a fixed electrical polarity in coelenterates where also, with one exceptional species, the growing end is electropositive.

The second condition also has been shown to be in accord with the facts. Newly hatched earthworms, although very small in size, possess the same number of segments as adults and register the same voltage, end to end, as the adults (Moment, 1950b). The second condition, and to a certain extent the third as well, is further substantiated, though perhaps indirectly, by the work of Coates and Cox (1945) on the electric eel. They reported that the electric organs of the eels grow by the addition of more and more electroplaxes, one posterior to another (in much the same way that an earthworm adds segments), until a length of about 50 cm is reached. Subsequent growth is by the enlargement of the electroplaxes already formed (again the situation is like that in earthworms). During the period when the electroplaxes are increasing in number, the voltage produced by the eel increases also. With the attainment of the full number of electroplaxes the increase in voltage stops, although increase in length continues. Thus a large, mature eel will produce many times the amperes that a small one less than half its length will, but both large and small eels will produce the same number of volts.

In this connection, it is important to note that Marsh and Beams (1950) have found that it is not the amount of the current applied to a regen-

erating animal that is significant in inhibiting proliferation but the voltage.

In regard to the third point, Burr and Hovland (1937) have found that in normal development the voltage measurable between the ends of an animal does increase to an asymptote. In regeneration, as can be seen in figure 1 (Moment, 1949a), increase in voltage is relatively rapid at first and then gradually slows to a plateau after which there is no further increase.

The fourth condition, namely, that proliferative growth in a terminal growing zone should slow to an asymptote at the same time the voltage does, and that further growth should be by the enlargement of structures already present, has been substantiated in a variety of material. Burr found that the voltage reached its asymptote in Amblystoma at about Harrison stage 40, or slightly older, when it seems highly probable that, however the somites are formed, they have attained their definitive number. A study of 330 cases of *Triturus viridescens* has shown (Moment, 1949b) that the number of caudal vertebrae, at least in this salamander, is fixed when the animals are very small. Furthermore, unpublished studies in this laboratory on *Rana sylvatica* show that the number of caudal myomeres is fixed in tadpoles that are only about 10.6 mm long, and at a stage comparable to Amblystoma at 12 mm and stage 40.

Direct evidence of the parallelism in time of the slowing of proliferation and the decline in voltage increase has been found in earthworm regeneration (Moment, 1949a). Both processes run concomitantly, both reaching their asymptote approximately at the same time; while growth in length is a far slower process and continues long after increase in voltage and increase in number of segments has stopped (cf. fig. 1—Moment, 1949a).

An especially noteworthy support for the hypothesis that proliferative growth should slow down as the anatomical level of growth becomes more distal and the voltage consequently progressively greater, is found in what is known as "Morgan's law of regeneration." Apparently this phenomenon was first observed over 200 years ago by Spallanzani, who noticed that the rate of regeneration in salamander limbs and in tadpole tails bears an inverse relation to the distance of the site of regeneration from the central region of the body. Specifically, he found that when the entire forelimb on one side of a salamander is amputated but only the toes on the opposite side, regeneration is so much more rapid from the shoulder than from the foot that an entire new limb will be formed from the shoulder in about the time required for the foot to grow merely the lost toes! Likewise with tadpole tails, the closer to the body is the amputation, the more rapid the regeneration.

This phenomenon was rediscovered over a century later in the regenerating arms of a starfish by King (1898) working in Morgan's laboratory. For *Asterias vulgaris* King reported, first, that regeneration takes place by proliferation at the tips of the arms and, second, that "the rate of regeneration is greatest from the disc, and decreases directly toward the tip of the arm." In the following decades Morgan (1906), Zeleny (1903, 1916), Mayer (1910),

and others extended these observations to many other organisms (coelenterates, polychaetes, teleosts) until this all-but-forgotten "law" had been shown to be valid for at least 27 species, distributed among seven phyla.

The early investigators were at a loss to explain these facts, except to say that the rate of regeneration is proportional to the "extent of injury." But this is clearly more of a restatement of the facts than an explanation, and in actual practice "extent of injury" became, as Zeleny showed, extremely difficult, if not impossible, to define.

Morgan himself (1906), rejecting the idea that regeneration slows down because of an exhaustion of the food supply, offered an explanation in the following terms:

> The new growth will come to an end when the last formed part has developed, whose differentiation is of such a kind that the resulting [mechanical] pressure, thereby established, no longer acts as a stimulus on the growing region to produce another new part. In the formation of a tail, the pressure reaction is a gradually decreasing quantity, and along with the decrease there goes a decrease in the stimulus to further growth [so] that it ultimately comes to an end. This analysis shows why there should be a gradual slowing down of regeneration as the normal form is approached, and it is apparent that this retardation will be the same whether it occurs near the end of an old part, or, as a new part approaches completion; for on the hypothesis, the conditions will be the same in each.... The most problematical part of the hypothesis is, I think, the assumption regarding the nature of the influence of the formed part. I have assumed this to be a pressure relation of some kind, possibly some other condition may be found....

This "pressure relation" theory suggests in a very general way the present theory of the progressive inhibition of growth by increasing electrical potentials in progressively distal regions. In any case, the four conditions stated at the beginning of this section as necessary for the validity of the self-produced inhibitory voltage system are met by the facts.

One additional question about anatomical and electrical correlations arises. Are the effective voltage-producing units the segments, or are the segments, after a very early stage in their development, merely convenient indicators of regions each composed of approximately the same number of cells, which are the effective units? Evidence is accumulating which strongly suggests that the effective voltage-producing units are individual, electrically polarized cells.

This does not imply that all the cells of the body would be supposed to contribute to the voltage existing between the ends of an animal, or that all cell division would be blocked by that voltage. Cells which did not lie in a distal zone and which had differentiated in such a way that some proliferation is still possible would be expected to continue to divide. Blood cells, chloragogue cells, and the germinative cells of the epithelia of the gut, skin, and the gonads, are such. Cells of this type are highly sensitive to control by hormonal and nutritional factors. Nor is it easy to see how cells like those of the blood, or of the epidermis, which are known to be electrically polarized in an inside-outside axis, would play much part in the voltage existing between the ends of an animal.

No one has shown that segments are electrical units, but on the other hand, cells are well known to be. Furthermore, the limbs of vertebrates

where "Morgan's law" holds are not segmented in any strict sense, but they are of course cellular. Evidence has been accumulated in this laboratory that the small young segments of annelids that give the same voltage as the large, mature segments actually possess the same number of cells. It is easy to show in any small aquatic oligochaete stained in toto by the Feulgen method, that the number of cells becomes fixed very early, while the segments are extremely small, and the subsequent growth is by cell enlargement. It has also been shown in earthworms that the muscle cells of the gizzard (a structure anatomically similar to the general body musculature of the earthworm, but in which cell counts are relatively easy), the cells of the nephrostomes, and various other structures do not increase in number after hatching (Moment, 1950a).

This evidence for the existence of a definitive cell number in various oligochaetes agrees with the work of MacCallum (1898), Schiefferdecker (1919), and others that in mammals the number of muscle fibers and nuclei becomes fixed long before birth, and with the work of Allen (1912) and others since that time, that there is little if any cell division in the mammalian nervous system after birth.

The only available evidence against the idea that the individual cells are the effective units appears to be the situation found in polyploid salamanders by Fankhauser (1945). In these animals the cells are much larger than in normal diploid animals, yet the size of the body as a whole and of the various organs is at least very close to normal. This is due to a reduction in cell number. In an earlier paper, Fankhauser (1941) suggested that this might be because there were fewer cells in the egg at the end of cleavage, or that it might be due to the slower division rate of polyploid cells.

In terms of the self-produced inhibitory voltage theory, at least two possibilities present themselves. It might be that polyploid cells are more sensitive to an inhibitory voltage than normal cells, and hence stop dividing when a lower voltage has been attained. The slower division rate of the polyploid cells suggests that they may be more easily inhibited. This would result in fewer cells; but since the cells are larger than normal, body size would be relatively unaffected. It is also conceivable that polyploid cells produce more voltage than normal cells.

ON THE LIMITATIONS OF NUTRITIVE THEORIES

That some cells may possess nutritional advantages over others has been known for many years. In spawning salmon, for example, the gonads develop at the expense of muscles but not of the nervous system (Lusk, 1909). More recently Robb (1929) attempted to explain the relative sizes attained by different structures by a "partition coefficient" according to which certain cells have an assimilative advantage over others. This general concept was utilized by Twitty and Schwind (1931), Huxley (1932), Moment (1933), Barth (1938), and Spiegelman (1945) to account for growth differentials.

On the descriptive level at least, it is possible, as Robb and Spiegelman have shown, to express the degree of any nutritive advantage possessed by

one type of cell with considerable mathematical precision. In a starving hydroid or other animal, it can readily be supposed that the relative growth of the various organs is determined by the competitive interplay between cells of differing assimilative capacities. However, although these ideas are true as far as they go, they are quite inadequate to account for the observed facts.

In the first place, the statement that the cells of a distal proliferating zone stop dividing because they have lost their assimilative advantage over the rest of the cells requires important qualifications. In earthworms (Moment, 1950a) and in other animals where this has been studied, the segments and cells stop increasing in number only. In well-fed individuals the small segments, and the small cells of which they are composed, thereafter increase in size by many hundred per cent both in normal development and in regeneration. Even in starving animals they continue to increase in size. This can only mean that if proliferation slows down and finally stops primarily because of some loss in nutritional advantage, it must be a loss of some nutritional advantage which is essential for growth by cell division but clearly not necessary for growth by cell enlargement. Much of the work done on partition coefficients in relation to organ growth concerns stages so late in development that chiefly growth by cell enlargement is involved. This was true of the work by the present author (Moment, 1933) on the relative growth of various organs in rats growing at different rates. In most cases not enough is known about the time when growth by cell enlargement becomes dominant to know which type of growth has been involved.

Equally important is the fact that it is possible to show experimentally that competition has no measurable effect on the rate or end-point of regeneration. Morgan (1906) was unable to detect any effect of competition between two or more regenerating parts in teleosts or amphibians. His results were confirmed and greatly extended by Zeleny (1916) and his associates in a long series of investigations on amphibians. Two decades later Twitty and DeLanney (1939) reached the same conclusions on the basis of experiments with amphibians in which they used the transplantation technique combined with amputations and starvation. Even the most drastic experiments, like causing the simultaneous regeneration of all four limbs, or limbs and tail in a starving animal, produce no measurable effect on the regeneration of any one part. In a long series of tests on an earthworm and on a polychaete (Moment, 1949c, 1951), it was impossible to show any effect of competition when the worms were regenerating from both ends simultaneously.

As to posterior regeneration in earthworms, it will be recalled that in the work alluded to earlier in this paper, a worm cut at the level of the 50th segment stops proliferating new segments at the distal growing zone when it possesses a total of 50 large old plus 40 small young segments. Under the same conditions a worm cut at the 80th segment will stop forming new segments at the proliferating distal end when it possesses a total of 80 large old plus only 10 small young segments. This is approximately true

even in worms under complete starvation. To explain these facts according to a nutritive theory, it is assumed that proliferation comes to an end *because* an equilibrium has been reached between the competitive nutritive abilities of the old mature cells and the young regenerating ones. But if this be assumed, it would seem to require the further and paradoxical assumption that 30 large old segments (numbers 51 through 80) in the second case possessed the same youthful competitive advantages as the corresponding 30 young regenerated segments in the first case!

The extent of the inadequacy of any theory of nutritive competition to account for growth limitation is nowhere more apparent than in the phenomenon of "Morgan's law" as seen in earthworms. In figure 1 (Moment, 1950a) it was shown, that, since all worms had regenerated for the same time, the rate of regeneration falls in a linear manner as the anatomical level becomes more distal, that is, posterior. Some internal growth-regulating factor or factors appear to be present which make growth increasingly difficult as the anatomical level of growth becomes more and more posterior. In the terminology of Spiegelman, the competitive nutritive advantage of the regenerating cells is becoming steadily less. In the terminology of Twitty and van Wagtendonk (1940), the regenerating cells are undergoing "physiological aging" of such a kind that their "assimilative capacities" are declining.

But on that theory the central question of growth regulation remains unanswered: what is it that so precisely controls the rate at which cells lose their "competitive advantage" or undergo "physiological aging"? Why do embryonic regenerating cells starting from the level of the 80th segment begin as old ones as compared with embryonic regenerating cells starting from the 50th segment? Nutritive theories give no answer; and in the long extent of these worms from the 50th segment to the 80th there are no evident anatomical differences. On the other hand, such a damping effect, ending in complete inhibition of proliferation, as the anatomical level of regeneration becomes progressively more distal, is exactly what would be predicted from the self-produced inhibitory voltage theory.

HORMONAL AND OTHER GROWTH REGULATING FACTORS

There can be no doubt that many factors influence the complex processes of proliferative growth. In the egg, the rate of cleavage, following Balfour's rule, is inversely related to the volume of yolk granules in the cells. In this and later stages it has been abundantly demonstrated that a long array of factors influence cell division: temperature, soluble nutrients, waste products, various enzyme inhibitors and accelerants, electrical potentials, hormones. It may even be that steroidal hormones are involved in all cell division, animal and plant, and that the sex hormones of the vertebrates are to be regarded as highly specialized examples of substances of general biological distribution and significance (Bullough, 1952).

The self-produced inhibitory voltage theory in no essential way conflicts with the facts and theories just listed. What it does is to suggest

that the electrical potentials produced by animals exert a limiting and overall regulatory effect on proliferative growth, that these potentials establish the perimeters, as it were, of the organism. Since a somewhat similar role has often been assigned to the hormones, especially the pituitary hormones, it seems appropriate to discuss them at this point.

The dramatic effects of hormones on growth are too well known to need illustration here. The equally remarkable limitations of the hormones appear to be less well known. These limitations are nowhere more clearly demonstrated than in the meticulous and extensive investigations of Blount (1932, 1935) on the salamander Amblystoma. In this animal it is possible to remove the entire pituitary gland at an early stage of embryonic development. Such hypophysectomized animals continue to develop but remain a peculiar pale color because their melanophores never expand normally. Their thyroid glands remain underdeveloped; consequently they never metamorphose. Their gonads remain juvenile. Nevertheless, the growth of the animal as a whole proceeds in an approximately normal manner. By the time the larvae are fully developed and at the size when metamorphosis should occur, the hypophysectomized animals are almost indistinguishable from the normal except in color. On the average the hypophysectomized animals are smaller than the controls, but they may be slightly larger. Individuals into which two additional pituitaries have been grafted are much darker than controls and are regularly smaller than either control or hypophysectomized animals. Thus, although pituitary hormones modify growth in these animals, the extent of this influence is strictly limited.

A similar situation is evident in rats. Hormone injections will increase body size to a certain point, beyond which no further increase occurs. Hypophysectomy produces stunting. But since both of these procedures are performed after birth, by which time the number of muscle fibers and nuclei and of nerve cells has become fixed, such effects are exercised only on cell enlargement in these systems. Hoskins (1947) has noted in this connection that the growth factor is just as abundant in the anterior lobes of adult cattle as in those of calves. This strongly suggests that some other factor in addition to the growth hormones of the pituitary regulates growth. In regard to the skeleton, it is possible to see in published photographs of prepared skeletons and in X-ray pictures that the number of caudal vertebrae is the same in hypophysectomized, normal, and pituitary-injected animals. Becks, Simpson, and Evans (1945) have described in detail characteristic histological differences between the epiphyseal regions of normal and hypophysectomized rats. However, in rats the epiphyses remain open throughout life (Dawson, 1927). What controls the length of the long bones in such animals remains an open question. The conclusion seems inescapable that the hormones are but one among various classes of factors that regulate growth.

POSSIBLE MECHANISMS

It would be of course premature to suppose it possible to write with any degree of finality about the details of the biochemical mechanisms involved

in electrical inhibition of proliferative growth. Nevertheless, any theory becomes more probable when a possible mechanism can be suggested, at least as a point of departure. And in this case enough facts are known to make possible some definite working hypotheses. A truly staggering amount of basic work has already been done by Lund and his associates. For a complete bibliography, see Lund (1947). Most of these investigations were primarily concerned with establishing the fact that bioelectric potentials are intimately involved with cellular oxidations. This concept seems now to be widely accepted. Lorenté de Nó (1947) emphasizes that the available evidence forces us to conclude that "the resting membrane potential of nerve is dependent primarily upon respiratory metabolism."

Despite a wealth of experimental data, often reduced to mathematical symbolism, Lund and his school hesitated to go beyond the most general (though insistent) statements to the effect that "the electrical pattern is intimately related to the morphogenetic processes and polar and vector properties of cell and tissue functions...[so as]...to act as a *directive force* in laying down of new structures, that is, growth, and possibly the orderly transfer of various materials in morphogenesis" (Lund, 1947).

The present theory of the self-produced inhibitory voltage can be regarded as a development of this line of thought in the direction of greater definiteness. By relating the voltage more closely with developmental anatomy, and by introducing the idea of a correlated increase of voltage and of inhibition until a critical value of complete inhibition is reached, it becomes possible to include a far greater number of facts within a bioelectrical growth theory—for example, Morgan's law of regeneration and the number of segments in numerous animal species. It also becomes possible to suppose a biochemical mechanism along the following lines.

As a distal proliferating zone becomes more distal, it becomes more electrically positive with respect to the rest of the animal, in other words, it becomes a region with fewer and fewer electrons. This means that it becomes a region of greater and greater oxidizing potential. Does proliferation then slow down and finally stop because conditions become increasingly favorable for oxidations? There is both new and old evidence to support such a view.

Reed (1947, 1949) has found that mitosis is blocked in plant meristems if the oxidation-reduction potential shifts so that the naturally occurring dihydroxyphenols become oxidized to quinones. Whether the quinones themselves are causal or merely symptomatic is uncertain. But his results have shown that the addition of suitable hydrogen donors (such as sulfhydryl groups) to restore a reducing potential will enable cell division to reoccur.

Similar facts have been reported by Van Fleet (1949), who noted especially that there are extractable antioxidants in proliferating nondifferentiating tissues, and pro-oxidants in zones where cell division has stopped and differentiation has set in.

These recent findings harmonize nicely with the work of Hammett and his school. Hammett reported (1933) not only that sulfhydryl groups stimu-

late growth but that his data gave a "clear cut demonstration that the site of direct action of the chemical equilibrium is specifically on the Proliferation phase as contrasted with the subsequent processes of Differentiation or Organization." Coldwater (1933) reported similar results in posterior regeneration in the oligochaete Tubifex.

It is worth noting also that Hyman (1940) and Child (1941) have reported that although respiration was found to be highest at the anterior (and in their terminology "dominant") end and showed a decreasing gradient as more posterior regions were reached, nevertheless in extreme posterior or distal regions the respiration rose again so that the entire gradient was often U-shaped. Since the present theory holds that a distal or posterior end becomes a region of greater and greater oxidizing potential as it becomes progressively more positive, these observations of Child harmonize with the proposed mechanism of inhibition.

SUMMARY

The theory of growth limitation discussed in this review holds that animals continue to grow by the proliferation of voltage-producing units until, by the summation of these units, whether segments or cells, a critical inhibitory voltage is built up. The formation of these units occurs in distal growing regions, and it is in such terminal zones that the inhibitory voltage finally attains a critical value. Subsequent growth of the segments and of the cells of which they are composed, is usually very great, but it is primarily by cell enlargement, not by cell proliferation.

This theory is based on the facts uncovered by a systematic reinvestigation, on a scale never before attempted, of posterior regeneration in an earthworm. It is also supported by a large number of anatomical, bioelectrical, and biochemical facts contributed by previous investigators. These are discussed, together with the relationship of this theory to theories of nutritive competition and of hormone action in the control of growth.

In brief, the theory that a self-produced inhibitory voltage sets the limits of growth may be rightly regarded as a development of previous growth theories in the direction of greater inclusiveness of facts considered, and of greater definiteness in anatomical, physical, and biochemical specifications.

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LETTERS TO THE EDITORS

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HERBARIUM SPECIMENS AS RECORDS OF GENETIC RESEARCH

Some years ago, Dr. M. J. Murray published a study of the genetics of sex determination of the Amaranthaceae, based on a formidable program of experimental crosses between monoecious and dioecious species[1]. In preparing a taxonomic revision of a section of Amaranthus, I have just had occasion to examine this set of specimens and believe that a few of the species used in Murray's crosses were incorrectly identified. The following changes in identification are indicated:

"*Amaranthus hybridus* L., Angol race" should be *A. quitensis* H. B. K.
"*A. Hybridus* L., line 56" should be *A. Powellii* S. Wats.
"*A. caudatus* L., Mexican race" should be *A. cruentus* L.
"*A. caudatus* L., Manchurian race" should be *A. leucocarpus* A. Wats.

The criteria by which these species may be recognized are presented in detail elsewhere[2].

Since Murray used the four names in question in his published report, publication of these revised identifications may be helpful in interpreting his results. For example, the highly sterile F_1's and easily obtained amphidiploids from some of his "intraspecific" crosses become less remarkable when the crosses are described as interspecific, in accord with the revised identifications.

However, my main purpose here is not to discuss specific factual details of Murray's findings, but to call attention to his method of procedure as a case study in identification of research material. His first step in identifying his material was a common practice. Not being a taxonomist, Murray sent examples of the parent species used in his crosses to an outstanding taxonomist, Paul C. Standley, for identification. Standley has contributed more than any one else towards clarifying the taxonomy of the New World Amaranthaceae and is still the most competent authority on the greater part of this large group. No more apology is needed for Standley's occasional unacceptable identifications than for any pioneer work which is modified by later more intensive study.

Not content with even the best available authority, Murray took a second precaution in establishing the identity of his material, by preserving the herbarium specimens already mentioned. By the simple device of pressing a few dozen examples of the parental species and some of his hybrids, he effectively safeguarded results based on years of work with over 50,000

plants. Any qualified person who questions the identity of this material has only to send for the specimens in order to see for himself exactly what Murray worked with and what he meant by each name he used. Thus any taxonomic changes required by increasing knowledge of the group become no more than minor details. There is no possibility in this case that an otherwise competent investigation will become meaningless simply because the identity of the research material cannot be established.

One would expect that, of all people, geneticists would be most clearly aware of the uncertainty and inadequacy of identifying the organisms with which they work by names or any other kind of verbal description. Yet there is no evidence in current genetic literature that the permanent preservation of experimental plant material, either as living cultures or herbarium specimens, is anything like a universal practice. There are no doubt some cases in which specimens have been preserved without published mention of their existence or place of deposit, but in such cases their value may be lost.

Many geneticists who fully appreciate these arguments may have been discouraged from preserving specimens by the fact that existing herbaria do not always have the space or the inclination to accept their material. It may be that solution of this problem will come by establishing special herbaria, controlled by the geneticists themselves. There would be advantages in escaping from conventional herbarium practices, particularly if the usual sort of specimens were supplemented by population samples, photographs, and other data, as has been suggested by Anderson (1951).[3] The usefulness of such herbaria would not end with verification of taxonomic determinations of research material. They would serve as storehouses for all the mass of unexploited data present in the specimens preserved from field collections or experimental plantings.

Again, Murray's work offers a case in point. His crosses were made and scored primarily to study the inheritance of a single character. Yet his material can be used to study the inheritance of other characters without repeating his enormous labor. His plants have been invaluable to me in recognizing previously unidentified natural hybrids which happen to duplicate some of Murray's artificial crosses.

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JANUARY 15, 1953

NEW "EVIDENCE" ON THE ORIGIN OF MAIZE

In a recent issue of the AMERICAN NATURALIST, Randolph[8] published a paper entitled "New Evidence on the Origin of Maize." It is appropriate to ask, "What new evidence is actually presented?" Space does not permit a point-by-point discussion of the paper, but a few comments on several of its statements and conclusions will be made.

To test the hypothesis of Mangelsdorf and Reeves[5] that teosinte originated as a hybrid between maize and Tripsacum, Randolph pollinated 612 ears of Mexican and Guatemalan maize with Mexican and Guatemalan Tripsacum. He obtained two hybrid seedlings. This is the only "new evidence" in his paper. The results merely confirm the well-known fact that maize and Tripsacum do not hybridize freely. They do not invalidate the hypothesis of a hybrid origin of teosinte, as Randolph assumes. Seventy-six per cent of the gametes tested in crosses were derived from tetraploid Tripsacum which, if previous experiments are a criterion, would not be expected to yield fertile offspring when crossed with diploid maize. A large proportion of the remaining gametes were derived from *T. maizar* which, because it has knobless chromosomes and is more maize-like than teosinte in many of its characteristics, is not a good putative parent of teosinte. Further, the modern maize varieties used in these experiments are certainly not the maize exposed to hybridization with Tripsacum several thousand years or more ago. Randolph's experiments are not a critical test of *any* hypothesis and, in fact, are essentially meaningless.

In his discussion of "cytological evidence," Randolph states that there is a difficulty in understanding how terminal chromosome knobs of Tripsacum or teosinte might become intercalary if transferred to maize. Admittedly the cytological mechanism by which this may happen is not well known. However, according to the hypothesis supported by Randolph himself—that maize, teosinte, and Tripsacum descended from a common ancestor—many changes in knob position have occurred by some means.

Although Randolph places strong reliance on Longley's studies of numbers and positions of chromosome knobs in the American Maydeae, he seems to be unaware of Longley's[3] description of a type of tenth chromosome in maize which has an additional piece, approximately the length of the short arm, attached to the end of the long arm. The existence of this abnormal tenth chromosome has been amply verified by later reports. A similar condition is known to occur in teosinte.[2] If Longley and later workers are correct in their conclusion that an additional piece has simply become attached to the end of a chromosome, this suggests at least one possible method by which terminal knobs may become intercalary. Also, the data published to date[9] definitely show a correlation between high knob number in maize and proximity to Guatemala or to that general region. Although the relation of this correlation to the problem of the origin of maize is not completely clear, it at least suggests the possibility that some or all of the chromosome

knobs of maize represent introgression from teosinte, or indirectly from Tripsacum.

Randolph states that the possibility of a hybrid origin of teosinte can be dismissed without further consideration on the basis of cytological evidence alone. He seems to believe that the differences between maize and Tripsacum in such chromosome characters as number, length, and arm ratios would prevent the exchange of genes between the two genera. The fact was established by Mangelsdorf and Reeves[5] and verified by Randolph himself that in F_1 and backcross hybrids the chromosomes from the two genera do synapse weakly, that they form chiasmata (as evidenced by the occurrence of trivalents at diakinesis), and that they do rarely exchange genes. Randolph's description of the cytology of maize-Tripsacum hybrids does not contribute a single fact which is new. The only real difference between his interpretation of cytogenetical results and that of Mangelsdorf and Reeves is in the point of view. He is impressed by the rarity of exchanges, while they are impressed by the occurrence of any exchanges at all. The occurrence of knobless-chromosome forms of Tripsacum in both South and Central America does not invalidate the hypothesis.

Randolph's paper also contains broad statements which ignore important evidence. Omitted are references to several pertinent bodies of data, two of which will be mentioned. (A) The genes of teosinte by which it resembles Tripsacum rather than maize are not distributed at random over the ten chromosomes, but have a tendency to be grouped in a few segments of certain chromosomes.[4] (B) In 55 morphological characters which have been studied, teosinte has been found intermediate between maize and Tripsacum, or similar to one of them, in virtually all characters.[5,6] If Randolph's conception of the origin of maize and its relatives is correct, these two bodies of data must be explained as coincidences which occurred against very great odds. As Stebbins[11] has stated, "It is difficult to see how such a situation could have arisen except through hybridization." Stebbins may also be right in his suggestion that the hybridization occurred earlier than Mangelsdorf and Reeves[5] postulated—at a time previous to the wide divergence of modern maize and Tripsacum from one another.

Randolph doubts that there is appreciable introgression between maize and teosinte but presents no evidence to support this doubt. It is an established fact that maize and teosinte hybridize naturally and produce fertile intergrades. The frequency of this occurrence is incompletely known and would be difficult to measure, but an occasional pollination of maize by teosinte produces hybrids which unless rogued before anthesis would be expected to lead to general introgression. The writer has seen maize-teosinte hybrid intergrades in fields of maize without searching for them. These were seen in Central America and Mexico, and were noticeable even in El Salvador, where teosinte is relatively uncommon. The plants and ears were unmistakable duplicates of hybrids produced under control. An example similar to this was previously reported from Mexico more than thirty years ago,[1] and the original report has been confirmed many times.

Randolph gives the opinion that teosinte should be maintained as a separate genus from maize and mentions certain morphological characters as having generic value. However, he does not state why their value is generic rather than specific. A point of view very different from Randolph's has been given in some detail by Reeves and Mangelsdorf.[10] If results of cytological and genetical studies can be applied to taxonomy in this group of plants, as they have been successfully applied in many others, there are good reasons for considering maize and teosinte as congeneric.

At this moment it seems possible that Randolph may be correct in his statement, reviewing the archeological literature, that maize originated in the general region of Mexico. Undoubtedly some of the recently published evidence is suggestive of this. But new discoveries in this field are being made rapidly, and the entire picture might be changed suddenly by additional discoveries in South America. Some of Randolph's comments on this topic are in agreement with conclusions previously drawn by Mangelsdorf and Smith.[7] Certainly it is too early to say that Mexico is the only center of origin of maize, and it is not difficult to agree with Randolph that this question is by no means settled.

Upon reading Randolph's paper, the present writer was unable to escape the conclusion that if nothing more is wrong with the hypothesis of Mangelsdorf and Reeves than Randolph has been able to prove, then the hypothesis is perhaps even better than its authors have supposed.

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HOMOLOGOUS SEX-LINKED MUTATIONS IN MAN AND OTHER MAMMALS

Some years ago, when reporting sex-linked hemophilia in dogs, the writer[1] pointed out that, with 39 different chromosomes available in the dog and 24 in man, it seemed a remarkable coincidence, to say the least, that in both species a mutation preventing normal clotting of the blood should occur in the sex chromosome. This is all the more significant because by all tests the hemophilia of dogs is physiologically indistinguishable from that in man. The purpose of this note is to draw attention to what may be a similar instance of homologous sex-linked mutations in man and another mammal, and to suggest that two such parallel cases reduce almost to the vanishing point the possibility of their being coincidental.

Drieux *et al.*[2] have reported an interesting mutation in cattle which they called congenital hypotrichosis with anadontia. The three calves described were apparently completely hairless at birth, but later acquired a sparse coat of abnormal hair. One of them began at 15 days to grow fine, soft hair, but the other two were still completely hairless at 5 and 6 weeks. One of these that was kept alive for about 6 months showed a few sparsely scattered hairs on the neck at 2½ months, and by 4 months of age such hairs were evident in most parts of the body.

The three calves were completely toothless at birth, but the one kept to 6 months had then only 2 teeth. These were placed symmetrically, one on each side of the upper jaw, in positions corresponding to those of the first molars. These calves had tongues larger than normal. They were described as hornless, but the descriptions show that development of the horns was merely retarded, and not suppressed. The hooves were normal.

Drieux and his associates concluded that this syndrome was caused by a sex-linked recessive mutation. Evidence to support that view consists of four facts: (1) all 3 calves were males; (2) the mother of one was a daughter of the cow that produced the other two; (3) these cows were crossbreds of Maine-Anjou-Normandy stock, to which the sire of the calves was completely unrelated, he being an apparently purebred Charollais; (4) this bull's calves by other cows in the same district, to a number exceeding 180, were all normal. The mother of one toothless calf also produced (by the same sire) two normal male calves.

This syndrome is almost identical with the sex-linked abnormality in man known as anhidrosis with anadontia, or anidrotic ectodermal dysplasia. Several pedigrees of it were reviewed by Gates,[3] all showing sex-linked inheritance. The longest of these, and perhaps the best known, is that of a family in Sind, now in Pakistan. From the combined reports of Wedderburn to Darwin, and of Thadani,[4,5] it seems probable that this peculiarity has been known in that family since about 1780.[6] In some pedigrees a few of the heterozygous women show some degree of the abnormality, but seldom the full expression that is characteristic of males. The affected men have few teeth or none. They have a deficiency of hair, or abnormally fine, soft

hair, some becoming bald early in life. Axillary hair is similarly abnormal or absent. They lack sweat glands in the skin, and, as a result, experience great discomfort in hot weather. Their faces are shortened, presumably as a result of the absence of teeth, and the lips are thick.

It seems clear that the abnormality in the French calves differs little, if at all, from that in man. Since normal cattle do not perspire through the skin, the malfunctioning of sweat glands in these three toothless calves would not be evident in the living animals. Fortunately, sections through the skin were examined microscopically, and these showed that the sudoriparian (sweat) glands were cystic and lacked the secretory tubules normally present. Clearly, if cattle did sweat, these could not have done so. The enlargement of the tongue to which Drieux *et al.* referred may have been accentuated by shortening of the face in these calves similar to that in men showing the same mutation.

Apart from this mutation, three genetically distinct kinds of hypotrichosis are known in cattle.[7] In all three the teeth are normal, and all three are autosomal. This seems to add some significance to the fact that in this species a syndrome involving both hair and teeth is apparently sex-linked like its counterpart in man. However, there may be another hereditary defect of hair and teeth in cattle for which the genetic basis has not been determined.[8]

While the facts presented by the French investigators suggest a sex-linked mutation rather than an autosomal one, further evidence is desirable. It is pertinent to mention that Drieux *et al.* made no reference to the corresponding abnormality in man, and hence, when postulating a sex-linked basis for the defect in their calves, were presumably unaware that an apparently identical mutation is sex-linked in man. The parallel seems all the more remarkable because the sex chromosome is 1 of 24 in man, 1 of 30 in cattle.[9]

Considering this case and the hemophilia, one is tempted to speculate about the significance of homologous sex-linked genes in mammals of widely different orders, but discussion might perhaps be postponed pending the discovery of additional cases. Unfortunately, while a good number of sex-linked mutations are known for man, they have thus far been conspicuously rare in other animals. It is possible that a deliberate search in common laboratory animals for abnormalities known to be sex-linked in man might be worthwhile. The most common of these is red-green color blindness, which occurs in 5 to 8 per cent of males in different populations. Unfortunately, search for mutations affecting color vision would be complicated not only by difficulties in devising satisfactory tests for large numbers, but also by the fact that in mammals other than primates color vision is apparently not well developed.[10] It may be that in these mammals, the situation is the reverse of that in man, so that the "normal" animals are blind to red and green, and the mutants able to distinguish between these colors.

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PUBLICATIONS RECEIVED

THE AMERICAN NATURALIST is glad to acknowledge here the receipt of books on biological and natural history subjects which are likely to be of interest to our readers. No undertaking to publish reviews is implied in this acknowledgment. Books for notice may be sent to:

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Alexopoulos, Constantine John, 1952. Introductory mycology. 482 p., 187 fig. $7.00. John Wiley and Sons, Inc., New York.

A major problem for the instructor who attempts to present an introduction to the fungi has been to adapt one of the available text-books—which were apt to prove too compendious, too specialized in viewpoint, or too embarrassingly inaccurate—to the needs of such a course. That problem has been removed, in a remarkably satisfactory fashion, by Alexopoulos's book.

The author has begun with the incontrovertible opinion that what the student needs an introduction to is fungi; this is true however meager or great is his acquaintance with the general principles of cytology, genetics, physiology, ecology, or what-not. The text is therefore first of all morphological in emphasis; taxonomy, which is the grouping of organisms according to their degree of fundamental morphological similarity, and cytology, which in the fungi is scarcely separable from morphology anyhow, are similarly presented in some detail. The peculiarities of fungus genetics, which have so often proved a mystery to the students of diploid genetics, are adequately elucidated, as is the place of the several fungi in nature. Industrial mycology and pathology are sufficiently introduced.

The first group treated is the bacteria, not because they are held to be fungi, but because most mycologists want to know something about them (and, it may be, because it is so often difficult for the student to find adequate instruction in general, in contrast to pathological, bacteriology). After that come the four main groups of fungi, the Myxo-, Phyco-, Asco-, and Basidiomycetes, with the Fungi Imperfecti interpolated after the Ascomycetes. The Pyrenomycetes are treated together in a single chapter, with almost the minimum of subdivision—the state of our understanding being what it is, surely the best introduction to this great and poorly-known group. The examples are well chosen, from the viewpoint both of availability and current knowledge. Figures of structures and

developmental stages are well drawn, and in large measure are combined into excellent life-history diagrams. Special terms are well defined where they first appear, and there is also a glossary. The text is clear, readable, and well written.

The errors are few and not very serious. What one who still looks for an ideal text must chiefly wonder about is why the author should have burdened the major units in a conservative and sound classification with names that often are both anomalous and unfamiliar. The largest groups (below the kingdom) are called phyla, although by both custom and the terminology formally adopted by botanists they should be divisions. The endings of the names are said to be "standard for each category"; but "—mycophyta" is *not* the standard ending for divisions, even when they are recognized among the Fungi, nor is "—eae" for classes. For the rusts, smuts, and jelly-fungi the name Hemibasidiomycetes, previously used to designate only the smuts, has been revived to displace the well-established Heterobasidiomycetes, and Holobasidiomycetes is adopted, or perhaps invented, for the Homobasidiomycetes (hymenomycetes and gasteromycetes), even though as a descriptive term it applies quite as well to many of the Hemi- (that is, Hetero-) basidiomycetes. These, however, are aberrations that are easily rectified by whoever objects to them. They do not alter the fact that a usable and commendable introductory mycology text has been produced.

D. P. R.

Crocker, W., and L. V. Barton, 1953. Physiology of seeds. 267 p., ill. $6.50. Chronica Botanica Co.

Cross, William E., 1952. La estacion experimental agricola de Tucumân de 1914 a 1946. Trabojos e informer publicados. 714 p. Salvat Editores, A.A., Buenos Aires.

A brief account of the foundation and history of the Tucumân Agricultural Experiment Station by its former director. The greater part of the work consists of abstracts of the 458 published contributions made by Tucumân investiagtors. The value of the abstracts lies primarily in the fact that many of the original publications are now practically inaccessible.

Danielli, J. F., 1953. Cytochemistry. A critical approach. 139 p., ill. $4.00. John Wiley and Sons, Inc., New York.

This book is very largely a record of experiments carried out by Professor Danielli and those who have been associated with him. No attempt has been made to write a textbook. The reader is encouraged by emphasis on the need for rigorous procedures and by a certain liveliness in style to expect a critical approach to cytochemistry. "I do, however, hope that a good deal of what is recorded here may be regarded as in the nature of a blueprint for future developments in cytochemistry." Such high hope might be justified if the approach were truly critical. Perhaps the fairest appraisal of the book can be made by considering the most substantial chapter, that on the cytochemistry of alkaline phosphatase.

A reader familiar with recent work in this field will not find this chapter satisfactory. Too much is made to depend upon an unconvincing test for diffusion of the reaction products. Despite the author's assertions to the contrary, his test for diffusion has less relevance to the problem than the test carried out by Martin and Jacoby which leads to a conclusion contrary to his own. Danielli's results are also rendered suspect by recent experiments on the alkaline phosphatase content of isolated nuclei. Experiments on isolated cell components play an important part in cytochemistry. Such work must, of course, be considered critically, but in this book it is simply brushed aside. Professor Danielli's treatment of cytochemistry is often ingenious, but it is not painstaking and critical.

de Beer, G. R., 1953. Vertebrate zoology. 435 p., 185 fig. $5.50. The Macmillan Company, New York.

Esau, Katherine, 1953. Plant anatomy. 735 pp., ill. $9.00. John Wiley and Sons, Inc., New York.

In modern biology description and interpretation have increasingly emphasized dynamic and developmental relationships. Plant anatomy has been no exception, but the lack of a comprehensive text has long been felt. Students of plant structure and development will therefore highly welcome Professor Esau's book on the anatomy of seed plants. A leading authority in the field, she has re-assembled the basic subject matter of plant anatomy, with additional chapters on flower, fruit and seed, in this splendid and carefully documented volume. Arranged in a simple and logical way, the chief topics of anatomy are treated in a fashion which does not overemphasize the descriptive, functional and phylogenetic aspects, but employs to best advantage the methods which characterize the developmental approach. The results of modern fine-structural and experimental-morphological research have been well integrated throughout the book, and in posing or interpreting specific problems the viewpoint is generally dynamic and takes into account the unity of the organism. In this manner and through careful selection of old and new data a well-balanced synthesis has been achieved between classical anatomy and the interests and findings of the present generation of plant anatomists. The value of this publication for the teacher and for the investigator, who must often be overwhelmed by the vast body of isolated data in this field of botany, is self-evident and cannot be exaggerated. Numerous valuable references are given, and many excellent illustrations and superb plates support the text which is written throughout in a lucid and precise manner, a quality which is bound to insure the book widest use not only among students of plant anatomy and dynamic morphology, but also by their colleagues in other fields of biological endeavor.

R. B.

Gleason, Henry A., 1952. The new Britton and Brown illustrated flora of the Northeastern United States and adjacent Canada. 3 Vol., $30.00. New York Botanical Gardens.

As its title indicates, this work is intended to replace the Britton and Brown Illustrated Flora, now out of print and long out of date. More than a new edition, it is in fact a completely new work. Each species is keyed, described, and illustrated, the drawings as well as the keys and descriptions being original. Synonymy is restricted to the names occurring in other standard works relating to similar or adjacent regions. 4660 species, with many varieties and occasional subspecies and formae are included. Some of the more difficult groups are provided with two keys, one natural and the other artificial, or one for use with flowers and the other with fruit. Treatments of the Pteridophyta, the families Alismaceae, Caryophyllaceae, Compositae, Droseracaea, Iridaceae, Najadaceae, Verbenaceae, and Violaceae, and the genera Astragalus, Crataegus, Oxytropis, and Salix are contributed by specialists in the respective groups. The remainder of the work is that of Dr. Gleason.

D. D. K.

Hall, R. P., 1953. Protozoology. 682 p., ill. $13.35. Prentice-Hall, Inc., New York.

This is a fine book, but there is nothing fancy about it except the price. It is lavishly illustrated, but always with line drawings, clearly and neatly re-drawn from a diversity of sources; there are no colored plates, no half-tones, no coated paper. Even the printing has been skimped so that the rich bibliographies are reduced to skeleton citations of journal and page. The content is standard protozoology, with morphological, physiological and parasitological emphasis, and with a nice synthesis of modern studies. The first three chapters are on morphology, reproduction and classification; these are followed by a taxonomic review to the family level; then by chapters on physiology, heredity, host-parasite relationships, protozoa of the digestive and urogenital tracts, blood flagellates, malaria, and immunity and resistance. There is, for the naturalist, a curious failure to give any attention to the ecology of protozoa (except for the parasites); they are dealt with as laboratory organisms with scarcely any reference to their role in the sea, in the soil, or in the endlessly diversified fresh water habitats. That surely also is a part of protozoology, though it seems to hold little interest for our protozoologists.

M. B.

Hill, George W., 1952. The Radiant Universe. 489 p. $4.75. Philosophical Library, New York.

Lowrie, Walter, 1953. Enchanted Island. 200 p. $3.00. Philosophical Library, New York.

Moody, Paul Amos, 1953. Introduction to evolution. 475 p., ill. $6.00. Harper and Brothers, New York.

This is intended as a textbook for a general course in animal evolution, presupposing no previous biological training. It is thus in competition with the recent book by E. O. Dodson and the 1951 revision of the text

by A. F. Shull. The differences among them seem to be chiefly matters of emphasis and arrangement, with Shull (naturally) stressing genetics and Moody (naturally) including a chapter on serology. The Moody volume is built around a review of the evidence for evolution (298 pp.) from geology, geography, classification and morphology, with discussion of process largely confined to the last third of the book. It is mostly written in the pedestrian prose conventional for American texts, but there is a final "open letter to students" on theology and evolution written with delightful informality. If this had been placed first, and used to set the tone of the book, we would really have a "different" text.

M. B.

Nelsen, Olin E., 1953. Comparative embryology of the vertebrates. 982 p., 380 fig. $8.00. The Blakiston Company, New York.

This text presents a comprehensive, detailed description of vertebrate development, including the later stages of development usually studied in comparative anatomy. The use of this very long text in short courses in embryology will necessitate the omission of parts of the book. However, the integrated presentation of material makes selective omission very difficult and as a consequence it may not prove to be a popular text in elementary courses. Selected bibliographies, detailed chapter outlines, a good index, and numerous excellent illustrations all enhance the value of the book for both beginning and advanced students. With some difficulty the text might also be made to serve as a laboratory guide. Priced at $8.00, the book is a bargain.

C. L. M.

Rawlins, T. E., and William N. Takahashi, 1952. Technics of plant histochemistry and virology. 125 p. (offset) $3.50. The National Press, Millbrae, California.

Remington, John Stewart and Wilfred Francis, 1953. The composition and assaying of minerals. 127 p. $5.50. Philosophical Library, Inc., New York.

Russell, R. C., and D. H. Macmillan, 1953. Waves and tides. 348 p., ill. $6.00. Philosophical Library, New York.

Tegnaeus, Harry, 1952. Blood-Brothers. 182 p., ill. $12.00. Philosophical Library, Inc., New York.

Mr. Tegnaeus has made a distribution study of the phenomenon of blood brotherhood as it appears in various parts of the world, but particularly in Africa and Europe. His approach is on the whole scholarly and his references commendably exact, but some of his assumptions are questionable, to say the least. He lumps together an alliance for a specific purpose signalized by a blood pact with a mutual assistance pact of indefinite duration and covering all phases of life. This does not strike me as conceptually justified. Also he fails to make clear in all cases

whether the blood pact is or is not intended to create an artificial kinship analogous to an actual one. But these are minor blemishes in an otherwise useful and interesting work. This reviewer wishes to enter a protest against the too lavish format and consequently the too high price of such books as this. There is no need for it to be printed on high-grade clay stock in quarto size with numerous half-tone illustrations which add little or nothing to the reader's comprehension of the material, and above all, no need for it to cost $12.00.

S. P. D.

Tiffany, Lewis H., and Max E. Britton, 1952. The algae of Illinois. 407 p., 1183 line drawings in 107 plates. $10.00. The University of Chicago Press, Chicago.

This work is definitely more than a local algae flora. It "is designed as a research reference to common fresh water algae...and as an aid for the beginning student of phycology." The species which are described are generally widely distributed so the book should be a useful tool for most systematists of the algae. The nearly twelve hundred illustrations are particularly valuable.

C. Z.

Wardlaw, C. W., 1952. Phylogeny and morphogenesis. 536 p., ill. $7.50. St. Martin's Press, New York.

As the title indicates, this book reflects the two major interests of the author, who is a student of F. O. Bower and is well-known for his experimental morphological work on the shoot apex of ferns. This he describes extensively, while other chapters deal with various aspects of plant morphogenesis, such as growth substance relationships, the effects of genes on development and differentiation, physical factors and mathematical considerations. It is Professor Wardlaw's contention that plant morphogenesis not only "occupies a central position" and "must draw on the whole corpus of botanical knowledge," but also that phylogeny is "*the* most comprehensive biological theme." There should be a progressive synthesis between the two, and morphogenetic study therefore should not be pursued without application to the problems of phylogeny. These problems are presented at some length in sections on phyletic methods and comparative studies of ferns and other classes of pteridophytes, on the origin of a land flora, and on the changing theories which have to do with the morphological organization types of higher plants. Some examples are given of how phylogenetic and morphogenetic knowledge may benefit from each other. Here is a book which poses the problems of the dynamics of plant form in two ways: in relation to phylogeny and in relation to factors of organization and environment which control form in the individual. It not only provides useful data for further experimental morphological work, but also provokes thought as to the relationships between the morphological, morphogenetic and phylogenetic fields of inquiry.

R. B.

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SOME ENVIRONMENTAL AND CULTURAL FACTORS INFLUENCING THE STRUCTURING OF AUSTRALIAN ABORIGINAL POPULATIONS

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Theory in population genetics has been so vigorously developed in recent decades that its mathematical elaboration has run far ahead of its concrete applications to natural populations. Much of the theory requires empirical checking, yet this is difficult since the parameters which determine the characteristics of populations are generally ill-defined. There is great need to isolate and quantitatively evaluate the variables influencing the structuring of natural populations.

Man is sometimes considered an intractable subject for studies in population genetics. He is warm-blooded, produces few offspring, is long lived, and most important, his culture partially shields him from the forces in the natural environment. Nevertheless, properly chosen human populations may offer unusual research advantages. The aboriginal Australians are such an example. They are unique in that only in Australia did there survive into modern times an entire continent of peoples whose economy was based exclusively upon hunting and collecting, and whose culture was broadly uniform in terms of extractive efficiency. In ecological terms the aborigines represent a latter day survival of man at an essentially paleolithic level of economy, despite the presence of pressure-chipping, microliths, and stone grinding in some regions. Hence they are important as capable of revealing some aspects of the evolutionary processes affecting man in the Pleistocene, a period in which he passed through the definitive stages of racial differentiation.

Determinants of Australian aboriginal population structure fall into two broad categories: (1) cultural; and (2) environmental. Certain of the more obvious cultural determinants have been discussed in a previous paper (Birdsell, 1950). Aboriginal populations in Australia do not represent an amorphous pattern of biological family units, but are structured in terms of two larger social units, the horde and the tribe. The horde, or local group, is equivalent to an extended family, usually numbers about 40 persons, and is the primary land-owning unit. Throughout Australia the horde is exogamous, patrilineal and patrilocal; that is, a man takes his wife from outside his local unit, she lives with his horde, and their children belong to it. Thus in each generation 50 per cent of the local group gene pool is introduced from other hordes outside its boundaries.

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The Australian tribe consists of a group of hordes which are united by a common dialect, by a common attributed line of descent, and by a similar culture. No form of authority exists to bind the hordes of a tribe into a single cohesive unit, but its existence as a discrete social entity is recognized both by the natives themselves and by anthropologists. The tribe owes its existence to subtle forces of internal cohesion which are operative even at the low level of social integration characteristic of Australia. Territoriality, limitations on intergroup communication and on personal mobility doubtless contribute to defining tribal limits through lower rates of social interaction between distant hordes. In terms of the concepts of genetic space and genetic distance (Birdsell, 1950) the nature of population structuring is such that tribal boundaries operate as the essential barriers to gene flow, and probably act in most regions as barriers to cultural diffusion. Tindale (1940) has listed 574 aboriginal tribes for Australia. Brown (1930) estimated that at the time of discovery the total aboriginal population numbered 251,000 as a minimum, but more probably exceeded 300,000. Using Tindale's total for the number of tribes, these estimates give 437 and 523 upwards respectively for the mean number of persons per tribe.

If a genetic isolate is defined (see Stern, 1949, among others) as a population which forms a more or less closed group, so that its members are less likely than is expected by chance to exchange genes with members of another group, then the Australian horde, with its rapid influx of genic materials in each generation, does not answer these requirements. The tribe, on the other hand, as a socially self-defining unit, fulfills the essential requirements of the isolate.[1] Since population pyramids will be generally uniform from tribe to tribe, and tend to remain nearly constant through time, isolate size will be highly correlated with, but larger than, the size of the effective breeding population. A crude and preliminary analysis suggests that for Australia the size of the effective breeding population would be less than 40 per cent of the tribal population. Thus, the former would approximate but 40 persons for a tribe of 100; 200 for a tribal population of 500; and 400 for tribes totalling 1,000 natives. Hence the size of the effective breeding population in aboriginal Australia is small, and random genetic drift might be expected to be operative.

In an earlier paper (Birdsell, 1950) concerned with the construction of simple gene flow models for Australia, one of the primary simplifying assumptions used was that the average aboriginal tribal population was constant and approximated 500 individuals. Clearly not true when applied to

[1]The real determinant of rates of gene flow between groups is sanctioned sexual relations, which occur commonly between hordes and occasionally between tribes. Since it would be difficult if not impossible to measure directly, it may require indirect evaluation through differences in intergroup marriage rates. There are little published data at the level of inter-horde marriage rates. N. B. Tindale has prepared a manuscript providing the first comprehensive data on the frequency of intertribal marriages. This paper should assist in defining the rates of interisolate gene flow in Australia. There are some suggestions in the literature that the rate is higher between small tribes than between large tribes.

a small series of tribes, it was presumed to hold as a central statistical tendency when applied to large numbers of tribes. The present study is a result of the further investigation of this primary assumption.

MATERIALS AND METHODOLOGY

The basic materials for this analysis are derived from the excellent annotated Australian tribal map published by Norman B. Tindale (1940), my collaborator in the original field work of the Harvard-Adelaide Universities Anthropological Expedition of 1938–1939. In this paper Tindale briefly discusses the physiographic and ecological controls apparent in tribal distributions. He notes a high degree of correlation between tribal boundaries and ecological and geographical limits. Thus mountain ranges, divides, rivers, general ecological and plant associational boundaries, microclimatic zone limits, straits and peninsulas often furnish clear-cut and stable boundaries. In deserts the cluster distributions of hordes around the few permanent waters are equally clear, and waterless stretches delimit many tribal boundaries. Tindale (1940, p. 150) further stresses that "The general reverse relationship between size of tribal area and rainfall is marked." In qualitative form this important but not unexpected relationship is not an efficient predictive device.

The present investigation was begun in order to quantify the relationship between rainfall and the size of the Australian tribal area as a step in devising a method for evaluating the size of tribal populations.[2] First, the area was determined from Tindale's map for the 409 mainland tribes whose boundaries could be considered as reasonably established. The tribal boundaries are given as they existed just prior to the advent of white interference. This total series is shown by the combined hachured areas in figure 1. Tindale differentiated between well established and probable boundaries, but both classes have necessarily been used in this study. For 14 tribes portions of boundaries had to be arbitrarily assumed, and where possible these were based on natural ecological limits. Thus a slight, but unknown, degree of inaccuracy has been introduced in the identification of tribal limits. Since a closed spatial system is involved, this error may be presumed to be non-systematic, but it contributes to the unexplained variance in the correlation between the primary variables.

The determination of all areas was made with a Keufel and Esser planimeter, model No. 4236. The projection used for Tindale's map could not be determined accurately, but it seemed to be a compromise between equal area and equal distance systems. Empirical planimeter tests against areas

[2]After the completion of the present analysis it was discovered that N. B. Tindale had commenced a similar type of investigation using the same basic materials. After discussing this instance of parallel invention, we have decided to exchange materials at the data level, but to work totally independently at the conceptual level. Thus, when time becomes available, Tindale will publish his independent analysis, and Birdsell will publish his investigation in a more comprehensive and refined form than presented here. Opportunities for replicative research of this type are rare in the natural sciences, and the implications of these data are of sufficient importance to provide justification in this instance.

of known size (based upon 16 trials each, involving four replications of four different combinations of planimeter arm position, placement of the pole weight, and direction of tracing) gave one planimeter unit equal to 100.0 square miles ±1.0. The centers of the areas so tested ranged from 320 to 1,040 miles distant from the center of the map, and the three tests revealed no consistent system of distortion of area values proceeding toward the margins of the continent. It was therefore assumed that no error of importance would be introduced by using the above conversion value throughout Tindale's map.

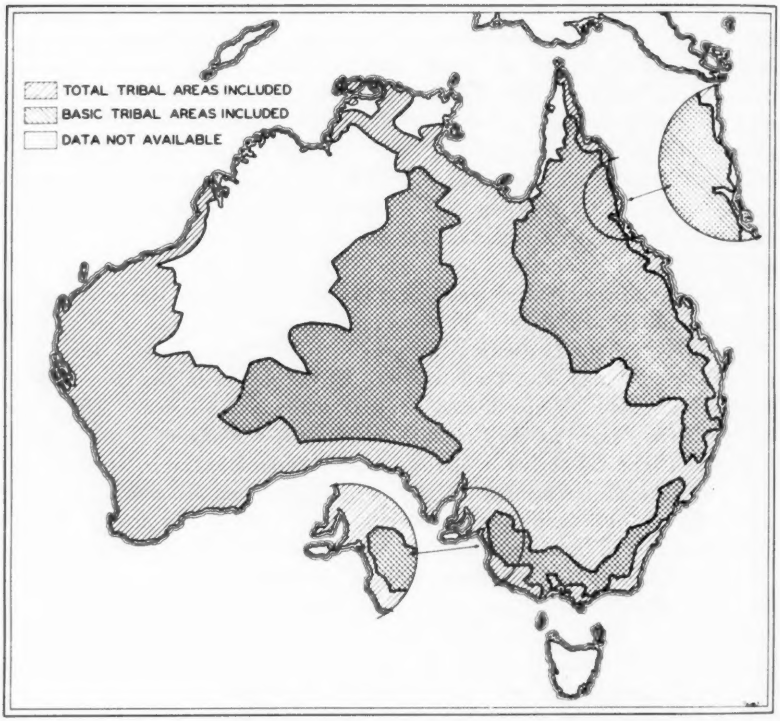

FIGURE 1. Distribution of total and basic series of tribes.

The area of each tribe was determined from the average of four planimeter runs, each involving either a change in the position of the pole weight, planimeter arm, or the direction of tracing. The range of the four values was usually ±1.0 planimeter units over a range between 10 and 500 planimeter units, indicating that the relative error of estimate decreased as the size of the tribal area increased. For very small tribes, with areas less than 10 planimeter units, the procedure was modified by extending each tracing of the boundary to five continuing replications, then dividing the resultant reading by five, and so obtaining a lower error of estimate.

In addition to the generally non-systematic errors introduced by the above operations, and which contribute to some small extent to the unexplained variance, there remains another possible source of error. This involves the definition and identification of the tribe as an entity. Tindale accomplished the enormous task of surveying the distribution of Australian aboriginal tribes with great skill, but he noted a number of difficulties encountered in the process. Much of the literature on the subject is filled with synonyms and confusing variations of tribal names. In many instances the earlier workers confused horde-like units with tribes. Tindale carefully evaluated these errors in nomenclature, and brought the data into a single, consistent system. Of the approximately 600 tribes on the continent, he obtained fresh information in the field on 400 tribal units, thus providing a sound matrix for the entire survey. Even so, other complications rendered his work difficult. He notes that tribal fragmentation seems to have occurred in three areas: (1) among the Murngin people of northeast Arnhem Land; (2) among the tribes along the Daly River in Northern Territory; and (3) in the Boulia district in central Queensland. On the other hand, consolidation among tribal groups seems to have occurred in the central interior of New South Wales, among such tribes as the Kamilaroi and Wiradjuri. This trend appears to reflect the development of a more advanced type of political organization based upon matrilineal descent. In addition to these regionally systematic variations, it is to be noted that sporadic shifts in the fortunes of individual tribes may result in their gradual differentiation into new multiple tribal units, in the case of growth in numbers, or their absorption into neighboring tribes in instances of declining population. Both tendencies alter the size of the tribal population, and hence the nature of intra-tribal and inter-tribal interactions. As pointed out in later sections, systematic regional deviations in either direction can be corrected for, but those of erratic occurrence cannot be excluded. Such cases result in increasing the unexplained variance of the size of the tribal area. The same will be true of those occasional cases involving inadequate data in which horde-like units have been elevated to full tribal status. In total effect these errors may have introduced a small systematic bias toward elevating portions of tribes to full tribal status. The size of this error cannot be estimated, but the thorough nature of Tindale's survey assures that it has been kept at a minimum.

Mean annual rainfall, the independent variable with which size of tribal areas is to be correlated, was obtained from a map modified after that published in the "Climatological Atlas of Australia" (1940 ?). The map is shown in figure 2. The method used in estimating the rainfall values for each tribal territory was crude but reasonably effective. It is analogous to estimating the center of gravity of an irregularly shaped and variably loaded plane surface. The "center of gravity" gives, through its position with respect to the isohyets traversing the area, the average mean annual rainfall for the tribal territory. In simple cases, as in arid regions, the estimate can be made rapidly by eye. In more involved instances, in which

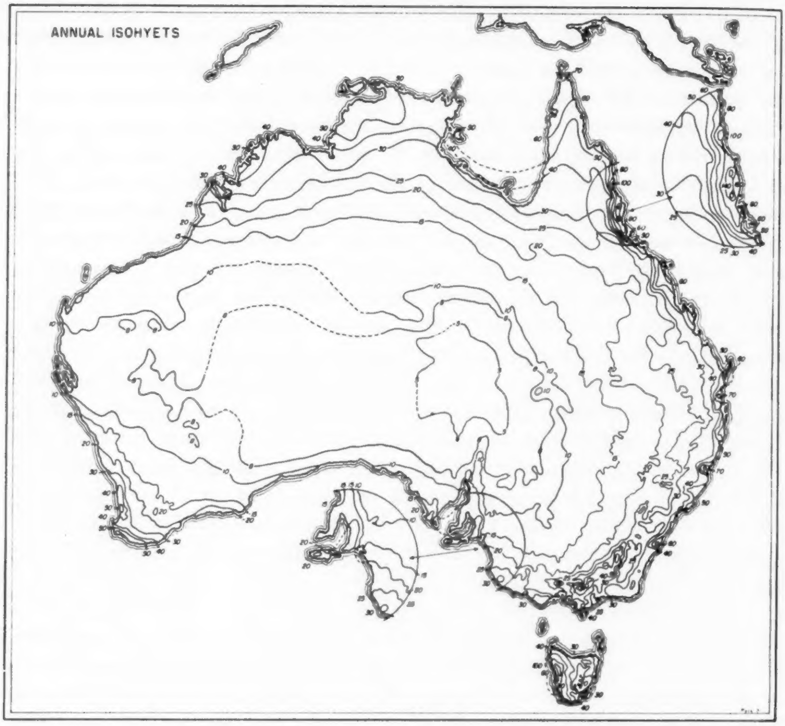

FIGURE 2. Distribution of mean annual rainfall.

several isohyets cross a single tribal area, the latter is broken down into a number of sub-areas, and the mean annual rainfall is estimated for each. The resultant average rainfall for the entire tribal area is then calculated by a method of weighted means.

To test the error of estimate, replicative estimates of rainfall were made along three transects which covered the full range of values from four inches to 150 inches annually. Each transect originated in the territory of the Wonkanguru in the Lake Eyre Basin, an area of minimal rainfall: the first extended north to the Njangga tribe on the Gulf of Carpentaria; the second stretched northeast to terminate in the rainforest with the Mamu tribe; and the third ran a little south of east to end in Dainggati tribal territory on the northern coast of New South Wales. Thus 33 tribes were subjected to re-estimation. In 23 cases the estimates of mean annual rainfall taken to the nearest inch were identical in the two trials. A brief analysis of the error of estimate gives approximately a mean error of ±1.0 per cent distributed over the total 33 cases. The value of the error was roughly constant over the total range of rainfall values.

A further source of error in the independent variable results from the generalized nature of the map used to estimate rainfall. In the few tribes

where it has been possible to check against more detailed data, the error from this source was sometimes appreciable. It is hoped that in a future analysis it will be possible to obtain data giving more accurate microgeographical rainfall values than those here used from necessity. Yet another source of possible error lies in the factor of time. Current rainfall estimates are based primarily upon records of 50 years or less in duration. In the older settled area of the south and east the tribal boundaries are given as they existed a century or more ago. To the extent that slight climatic shifts may have occurred in this ill-defined time interval the estimate of current rainfall may be systematically in error.

Beyond Tindale's comment that a general reverse relationship exists between the size of tribal area and rainfall, and the fact that his map shows it quite clearly, there are good theoretical reasons to expect such a correlation. In mammalian ecology it is generally recognized that the density of a given type of population will be some function of the critical environmental variables. While this relationship has not previously been demonstrated quantitatively for man, it seems likely that for hunting and gathering peoples similar forms of environmental determinism might obtain. In aboriginal Australia, with its moderate temperatures and small altitudinal variations as compared to other continents, it might be presumed that the biotically effective quantity of rainfall would prove one of the more important of the variables of the environment.

There remains the important problem of functionally relating the size of the tribal area to density. There is no reason for rainfall directly to determine the area occupied by the Australian social unit known as the tribe. Unfortunately there are too few estimates of the population size of aboriginal tribes to work directly with density as the dependent variable. The bridging device is found in the definition of population density as the number of individuals per unit of area. It follows that an exact inverse relationship is established between tribal area and tribal density if the population size of the tribes is held constant throughout this series. Thus it becomes crucial for the following analysis to make the intervening assumptions that: (1) population densities are causally and inversely related to the mean annual rainfall within the tribal territory; and (2) in a statistical sense the population size of the Australian tribe may be considered a constant, in this case approximately 500 persons. If the mean annual rainfall, which is the best simple measure available for biotically effective rainfall, does in fact show a reasonably high degree of correlation with the size of the tribal area, it will tend to validate both of the foregoing interlocked assumptions.

Since a certain rashness is apparent in the above statements, further explanations and qualifications are in order. The degree of correlation between two variables merely demonstrates the degree of association, and may or may not indicate a causal relationship. In the present instance as later evidence will show the ecology of the aborigines clearly argues that such a relationship is causal in nature. A further qualification must be

added with regard to the interpretation of such a correlation. If other critical parameters vary as some systematic function of rainfall, it would not be apparent from this form of analysis. Thus if the slight regional differences in aboriginal culture were to affect efficiency in extracting energy from the environment in some fashion associated with changes in rainfall, this complicating factor could not be identified in the primary correlation. Or if for any reason the average size of the tribal population varied as a function of rainfall, the distorting influence of this factor could not be detected. Thus, for example, tribes might have consistently small sized populations in desert areas, and larger ones in regions of high rainfall without this being apparent in the original correlation. But there is little evidence to suggest that this type of variation is important.

The scattergram showing the relationship between the size of the tribal area of the 409 tribes of the total series and their mean annual rainfall is given in figure 3. The distribution is by no means a random one, and shows a high degree of association. Several attempts at curve-fitting indicated that the data were satisfied by an exponential equation in the form:

$$Y = aX^{b}$$

where Y is the tribal area and X is mean annual rainfall. The coefficient of curvilinear correlation, rho, is 0.59 and σLog Y is 0.42854. Calculation of the constants gives the following equation:

$$Y = 615.00\,X^{-0.98980}.$$

The band of error calculated to give 95 per cent inclusion of the data is shown by the dotted lines in figure 3. It will be noted that rather fewer points fall outside than might have been expected. The logarithmic curve fits the central mass of the data fairly well, but in the asymptotic regions the data conform less closely to the curve.

A curvilinear coefficient of 0.6 for the unselected total series is encouraging, but from an ecological point of view the series is a heterogeneous one. Before proceeding to interpretation it seems wise to obtain an ecologically more homogeneous series by making certain types of systematic correction. Since our method involves assumptions that: (1) the size of the tribal populations approximates a statistical constant, and (2) that the size of the tribal area is an inverse expression of the tribal density, it will be advisable to eliminate systematically from further consideration those groups of tribes which show marked deviations from either assumption. Thus the categories of tribes subject to such exclusion may be chosen by two types of criteria: (1) systematic deviations from expected densities due to variation in ecological factors; and (2) deviations in either direction from the assumed constant size of 500 persons per tribe owing to the action of cultural variables. A validation for these categorical exclusions will be presented in later sections.

Ecologically, any environmental factors which alter the relationship between the area occupied by a tribe and the density expected for its rainfall regime will be considered grounds for exclusion. To provide the broadest

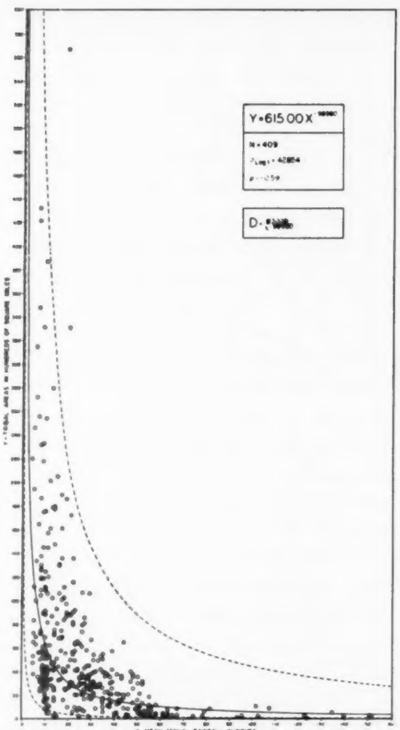

FIGURE 3. Correlation between rainfall and size of tribal area for the total series.

and most stable basis for comparison, our ecological standard will consist of those tribes whose resources are primarily terrestrial in origin, and whose territories are essentially watered by rainfall which falls within their territories. Those tribes whose domain lay wholly or partially upon islands were excluded prior to the creation of the basic series of 409 tribes. All coastally situated tribes are now further eliminated, since marine food resources would be expected to increase the population density compared to purely terrestrial tribal standards.[3] Just as marine food resources alter the usual density-area relationships, so will the foods provided by rivers. While much of the southern and western coasts, as well as nearly all of the interior of Australia, is characterized by intermittent or transient streams and rivers, there are coastal areas, particularly in the east and north, where permanent rivers are the rule. In such cases their waters are largely de-

[3]In a few instances in which the tribal territory included but a very narrow coastal strip, and hence only one or two hordes were presumed to reflect increased densities owing to the availability of marine foods, this criterion for exclusion was relaxed.

rived from small drainage areas, and the riverine food resources are considered here to be a normal manifestation of a high rainfall regime. But in the interior of the southeastern portion of the continent there exists a great and largely permanent river system, the Murray-Darling, which represents a rather different set of ecological conditions. There, in near-desert country, largely with less than 20 inches of rainfall annually, flow great rivers whose waters are derived from the western slopes of the Dividing Range. Insofar as the plains tribes of this drainage system are concerned, such rivers represent unearned surface water resources, since they are primarily nourished by rainfall from outside the plains country. Such riverine resources, like marine foods, alter the assumed relationship between the size of the tribal area and population density. For this reason, the tribes along the Murray and Darling Rivers, and their major tributaries, have been systematically excluded from the basic series.

From the cultural point of view, several factors operate so as to cause systematic deviations from the assumption that the size of the tribal population approximates a constant value of about 500 persons. Such deviations will disturb the usual relationship between size of tribal area and population density. As noted by Tindale (1940, p. 150) a group of tribes occur in the eastern interior of New South Wales in which a more advanced type of political organization, characterized by matrilineal descent, has allowed the development of especially widespread communities; that is, tribal entities in which the population size substantially exceeds 500 persons. He specifies the Kamilaroi and Wiradjuri as examples. Kryzwicki (1934) considered the Kamilaroi to have totalled between 6,000 and 7,000 persons and the Wiradjuri to have numbered about 3,000. His opinion was based upon rather unsatisfactory estimates by early settlers, but even though these tribal populations may have been overestimated, they must be eliminated from our basic series as essentially representing confederacies of tribes. Data for the neighboring Wongaibon tribe are less exact, but it too can be safely excluded owing to the systematic operation of cultural factors in this region.

Allowances by exclusion must be made for a further set of cultural influences. Tindale (1940, p. 150) indicated certain areas of postulated cultural clash, in which tribal fragmentation seems to have taken place, as exceptions to the generally inverse relationship between the size of tribal territory and rainfall. He specifies northeast Arnhem Land, the Daly River district of the Northern Territory, and the region around Boulia, Queensland, as examples of this tendency. These areas seem to reveal an intensified form of tribal fragmentation, but in a less extreme form the phenomenon is more widespread. The boundaries which separate the centrally situated circumcising and subincising tribes from the marginal groups which practice neither initiatory rite are shown in figure 7. An examination of Tindale's map reveals that the tribal areas lying just west of the eastern limits of the circumcising and subincising boundaries are notably smaller than those just to the east of the circumcising line. The Boulia district of fragmentation is just to the west of the there combined boundary lines.

Similar evidence for fragmentation associated with the spread of the initiatory rites occurs along their northern boundaries in the Northern Territory. Between the line representing the advancing front of the rite of circumcision and the less extended boundary of the subincision rite lie the two other areas of fragmentation mentioned by Tindale, the Daly River district and the Murngin region of northeast Arnhem Land. While these are focal points for the phenomenon of fragmentation, the same process seems to a lesser degree to have affected the other tribes which have recently taken over either or both of these ceremonies. Since in the case of neither the eastern nor northern limiting boundaries of the rites are there any visible ecological factors to explain the changes in tribal densities implied by the reduced size of the tribal areas, it must be presumed that the size of the tribal populations there is smaller than the assumed constant of 500 persons. The ethnological evidence for fragmentation tends to confirm such a conclusion.

The western boundaries of the rites of circumcision and subincision coincide. The signs of fragmentation expected to the east of the line are not visible from the map. As will be seen later, there are a number of possible explanations for this apparent difference. Nonetheless, to remove the potentially disturbing factor of fragmentation and consequently small-sized tribal populations from our analysis, a band of tribes lying just inside the limits of both the circumcising and subincising boundaries on their eastern, northern and western limits have been excluded from the basic series. While the width of the excluded band varies to some degree with the intensity of the fragmentation, in general it ranged three tribes deep inside the subincising boundary. The Boulia area, because of the extreme form of the phenomenon there, was treated more drastically.

Of the total original series of 409 tribes, 286 have been systematically eliminated from further consideration on the grounds that either ecological factors distorted the basic relationship between the size of tribal area and population density, or cultural variables produced undue deviations in the size of the tribal population as compared to the assumed constant of 500 persons per tribe. There remain 123 tribes which seem to be ecologically and culturally relatively constant in their characteristics, in so far as they effect this analysis. These 123 tribes constitute our basic series. As shown in figure 1 in the cross-hachured area, the basic series consists of three blocks of tribes: a large series numbering about two thirds of the total centered in Queensland; and two smaller groups of about 20 tribes each, one spreading through the desert area of the interior, the other extending through the southern portion of the Dividing Range to terminate in the west in the mallee scrub just short of the mouth of the Murray River. Thus the basic series, while ranging through nearly the full variation in rainfall, from five to 151 inches, is predominantly representative of the regional ecological conditions obtaining in non-coastal Queensland. In so far as the ecological variables for this region may not be representative for the continent as a whole, a systematic error may have been introduced into the analysis.

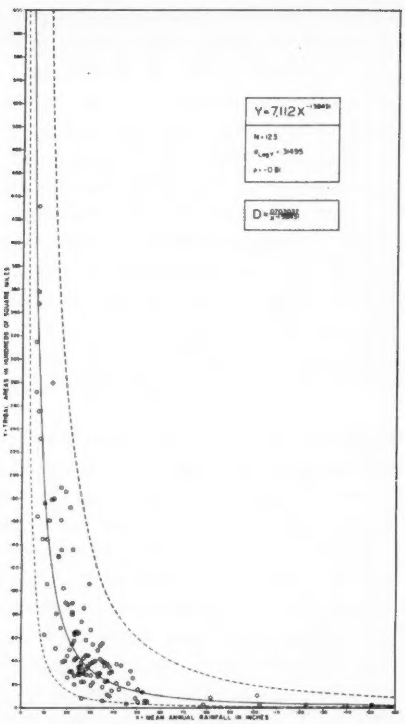

FIGURE 4. Correlation between rainfall and size of tribal area for the basic series.[4]

The scattergram showing the relationship between the size of the tribal area and mean annual rainfall for each of the 123 tribes of the basic series is given in figure 4. The distributional pattern is again that of a J-shaped curve, and these more cohesive data are likewise satisfactorily fitted by an exponential equation. Solving for the constants, the equation takes the form:

$$Y = 7{,}112.8\,X^{-1.58451}$$

Rho, the coefficient of curvilinear correlation, here reaches the very satisfactory value of 0.81. The band of error shown by the dotted lines, and calculated to give 95 per cent inclusion of the data, is derived from $\sigma =$ 0.31495. But 2 of the 123 tribes fall outside the band of error. This exponential curve, unlike that fitted to the total series, shows a more satisfactory relationship with the central body of the data, and more importantly with the data along both asymptotes. This improved degree of fit suggests that the systematic exclusions practiced in defining the basic series have

[4]The first constant in the equation in figures 4 and 5 should read 7,112.8 as in the text.

in fact diminished the heterogeneity of the data arising from ecological and cultural variables. The degree of displacement between the curves for the total and basic series is shown in figure 5. It must be inferred that there exists a very high degree of association between the size of the tribal area in the basic series and the mean annual rainfall occurring within its territory.

FOOD RESOURCES

Now it is time to reconsider the question of whether the association between these two variables is to be interpreted as causal in nature. Ethnologically it is well established that the diet of the aborigines in Australia is characterized by its broadly omnivorous nature. They consume all the edible animal and plant food in their environment which can be economically obtained and prepared by the techniques available at their cultural level. Examples may be quoted to give emphasis to this statement. Grey (1841), one of the most accurate of the very early recorders of native life, noted the following items of diet for the groups of tribes along the southwestern coastal region of Western Australia:

A. *Animal Foods*

(1) 6 sorts of kangaroos.
(2) 5 marsupials somewhat smaller than rabbits.
(3) 2 species of opossum.
(4) 9 species of marsupial rats and mice.
(5) Dingo.
(6) 1 type of whale.
(7) 2 species of seal
(8) Birds of every kind including emus and wild turkeys.
(9) 3 types of turtle.
(10) 11 kinds of frog.
(11) 7 types of iguanas and lizards.
(12) 8 sorts of snakes.
(13) Eggs of every species of bird and lizard.
(14) 29 kinds of fish.
(15) All saltwater shellfish except oysters.
(16) 4 kinds of freshwater shellfish.
(17) 4 kinds of grubs.

B. *Plant Foods.*

(1) 29 kinds of roots.
(2) 4 kinds of fruit.
(3) 2 species of cycad nut.
(4) 2 other types of nut.
(5) Seeds of several species of leguminous plants.
(6) 2 kinds of mesembranthemum.
(7) 7 types of fungus.
(8) 4 sorts of gum.
(9) 2 kinds of manna.
(10) Flowers of several species of Banksia.

This exhaustive inventory suggests that very few food resources in the environment remain unexploited. Two further dietaries may be quoted for reference. The first, from Sweeney (1947), lists the foods eaten by a single desert tribe, the Walpari. The second, from Roth (1901), details the wide variety of foods eaten by the coastal and interior tribes of Queensland. Such sample dietaries serve to substantiate the claim that the aborigines exploit all, or very nearly all, of the sources of energy culturally available to them in their environment, and cover the full range of food size which can be economically utilized. In a dry continent such as Australia, ranging from tropical to temperate climate, the variations in the flora will be de-

pendent to a large degree upon the rainfall received. It would be expected that the biomass of the flora would be correlated to a high degree and in a causal sense with the mean annual rainfall. The densities of aboriginal man, standing near the peak of the trophic pyramid and exploiting all lower levels, both animal and plant, must also respond sensitively to variations in rainfall. For these reasons it seems proper to assign a causal relationship to the high degree of correlation existing between the size of tribal territory in the basic series, and the independent variable, mean annual rainfall. The density of the aboriginal population in Australia was determined to a large measure by rainfall operating indirectly through the biota.

THE EXCLUDED MATERIAL

Since the basic series was created by systematic exclusion of certain groups of tribes which were considered ecologically or culturally to increase the heterogeneity of the data, it will now be profitable to reexamine the relationship of these categories to the basic series. Table 1 lists the excluded categories, and gives the mean area ratio and mean density ratio for each. The area ratio represents the measured area of the tribal territory divided by the area predicted by the basic equation for its value of rainfall. The density ratio is the reciprocal of the area ratio. In most instances it may be considered to indicate the ratio of the actual tribal density compared to the density predicted from the basic equation, based upon the assumed tribal population size of 500 persons. In a few instances, where the ecological factors remain essentially constant and the cultural factors vary, the density ratio must be interpreted as reflecting variations in the size of the tribal population rather than deviations in density. Thus an area ratio of 0.500 indicates that the tribe occupies but half the area predicted from its rainfall regime. This reduced area may either be due to ecological advantages in its territory, or to a population half the size of the expected 500 persons. The density ratio in this case would be 2.00, and might either mean the tribal density was twice that predicted, or that the size of the population was half that expected, depending upon whether the deviation is interpreted as resulting from ecological or cultural factors. In more complex instances both types of factors may be operative, but this possibility is necessarily ignored in the present analysis. While interpretations of this type cannot safely be applied to single tribes, it is considered that they may hold with some validity for systematic categories of tribes.

One of the most revealing categories of exclusion involves the ecological effect of unearned surface water upon population density. Unearned surface water in this sense refers to rivers, or freshwater lakes, which depend for their existence upon rainfall from distant regions. The Murray and Darling Rivers are the best Australian examples. Both originate on the relatively well-watered western slopes of the Dividing Range and flow through increasingly arid country. Much of their way lies through regions with but 10 to 15 inches of rainfall, and hence in their lower reaches the

TABLE I

EFFECTS OF ECOLOGICAL AND CULTURAL FACTORS UPON DENSITY RATIOS.

	Area ratios	Density ratios
1. Ecological Factors Changing Densities of Tribal Populations.		
A. Unearned Surface Water:		
(1) 9 lowest tribes on Murray River:	0.058	17.33
(2) 5 lowest tribes on Murray River:	0.026	38.46
B. Marine Resources of Islands:		
(1) 27 tribes partially or completely insular:	0.402	2.49
(2) 26 tribes (omitting Tiwi) partially or completely insular:	0.326	3.07
(3) 13 tribes completely insular:	0.349	2.86
(4) 12 tribes (omitting Tiwi) completely insular:	0.179	5.58
(5) 5 tribes with 20 to 65 per cent insular domains:	0.220	4.56
(6) 8 tribes with 0.005 to 10 per cent insular domains:	0.653	1.53
C. Marine Resources of Mainland Coastal Tribes:		
(1) Total available sample of 119 tribes:	0.751	1.33
(2) Southern coast: 8 tribes (Wirangu through Wardandi):	1.425	0.70
(3) Western coast: 17 tribes (Pindjarup through Ngaluma):	0.453	2.21
(4) Eighty mile Beach coast: 2 tribes (Njangamada and Karadjeri):	0.620	1.61
(5) Dampier Land coast: 7 tribes (Jauor through Ninanboro):	0.184	5.44
(6) Arnhem Land coast: 6 tribes (Wogait with 3 breaks through Gunavidji):	0.408	2.45
(7) Gulf of Carpentaria: 10 tribes (Nungubuju with 1 break through Karundi):	0.895	1.12
(8) Eastern coast Cape York Peninsula: 15 tribes (Ankamuti with 1 break through Koko-imudji):	0.586	1.71
(9) Rainforest coast of Queensland: 8 tribes (Jungkurara through Warkamai):	0.961	1.04
(10) Central coastal Queensland: 9 tribes (Bindal through Kabikabi):	1.267	0.79
(11) Southern coastal Queensland and northern New South Wales: 13 tribes (Jagara through Awabakal):	1.050	0.95
(12) Southern New South Wales and eastern Victorian coasts: 10 tribes (Kameraigal through Bratauolung)	0.671	1.49
(13) Western Victorian and eastern South Australian coasts: 14 tribes (Kurung through Nauo):	0.606	1.65
2. Cultural Factors Changing Size of Tribal Populations.		
A. Advanced Type of Political Organization:		
(1) The "confederacies" of New South Wales: 3 tribes (Kamilaroi, Wiradjuri and Wongaibon):	5.200	0.192

TABLE I (*continued*)

	Area ratios	Density ratios
B. Fragmentation of tribes due to Recent Acquisition of Circumcision and Subincision Rites:		
(1) Eastern Circumcision boundary:		
(a) Western side: 25 tribes affected (Jokula through Kaurna):	0.467	2.14
(b) Eastern side: 21 unaffected tribes (Kalibamu through Ramindjeri):	0.728	1.37
(c) Western side: 17 affected tribes between points A–B in Fig. 7. (Workabunga through Maljangapa):	0.286	3.50
(d) Eastern side: 13 unaffected tribes between points A'–B' in Fig. 7. (Kukatji through Wiljakali):	1.002	1.00
(e) Western side: 12 affected tribes (Workabunga through Ngandanjara):	0.318	3.14
(f) Eastern side: 8 unaffected tribes (Kukatji through Wadjalang):	1.334	0.75

rivers provide locally unearned ecological resources. Tindale (1940, p. 150) indicated that the fisher-folk of the Murray River enjoyed special food advantages. A quantitative analysis strikingly extends the meaning of his statement. In figure 5, the nine tribes of the lowest portion of the Murray have been plotted as hollow triangles in their appropriate positions. As compared to the basic curve, these riverine tribes show drastically reduced area ratios with the mean value of but 0.058. Their mean density is 17.33 times that expected from the local rainfall regimes.

Since all the tribes in the drainage of the Murray and Darling Rivers were eliminated from the basic series, it will be well to examine their position as a group. In figure 6, the area ratios of the tribes bordering on these two rivers have been plotted against their distance from the mouth of the Murray. The trend in the unaltered data was clear, but fluctuated sufficiently so that for plotting purposes the data were smoothed out by calculating the value of the area for each tribe from a moving 3-point average. Thus treated, the data show a consistent reduction in the size of the area ratios from the Pangerang tribe near the headwaters of the Murray to the Warki at its mouth.

In a similar if less striking fashion the area ratios of the tribes along the Darling diminish from the Koamu tribe near its headwaters (in actuality, on the Balonna River, a major tributary of the Darling), to the Maraura tribe situated at the junction of the Darling with the Murray. The curves shown in figure 6 were drawn freehand merely to indicate approximate trends, and a more detailed future analysis may modify their form considerably. The data show a consistent decline from the initially higher than normal values of the area ratios at the headwaters of the two rivers to the extraordinarily low values at the Murray mouth. While the data do not lend themselves to exact curve fitting, certain regularities show through. Those few tribes which include but one bank of the Murray in their territory uniformly show

FIGURE 5. Deviations of certain excluded categories of tribes from the basic curve.[4]

higher area ratios than those which include both banks. The three tribes nearest the Murray mouth show disproportionately low area ratios, perhaps as a consequence of bordering upon ecologically rich Lake Alexandrina. The five tribes nearest the mouth have an average area ratio of but 0.026, and the spectacular mean density ratio of 38.46. Since the population estimates available for these tribes, as summarized by Kryzwicki (1934) indicate that they have exceeded our assumed constant of 500 persons per tribe, it must be concluded that here the ecological effect of the unearned surface water of the Murray is responsible for aboriginal densities perhaps 40 times that to have been predicted from local rainfall values.

An ecological analysis of the Murray-Darling tribes cannot be attempted in detail at this time, but the region is obviously superior in its food resources. The waters of the river directly contribute a number of important food fish, shell-fish, and waterfowl. Indirectly the forested banks of the river increase the supply of birds and arboreal marsupials. The rich bottom lands offer a greater abundance of food plants. The ecological variables operating to increase human densities along these rivers cannot be identified in detail but it is obvious that such density ratios are not

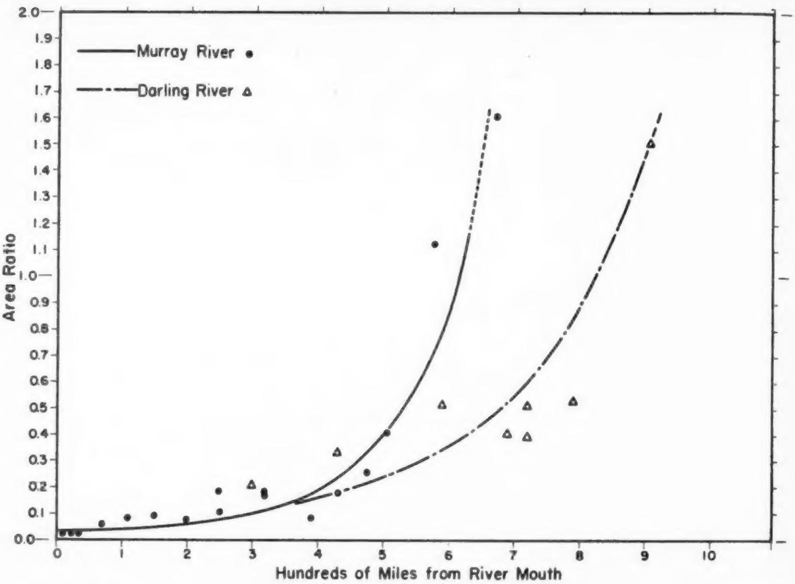

FIGURE 6. Area ratios of Murray and Darling River tribes plotted against distance from Murray mouth.

primarily determined by rainfall alone. The volume of water flow and its reliability may prove to be fair ecological indices. On the other hand, stream gradient appears to be correlated with aboriginal density and may be the primary factor. It may be postulated that the younger, steep-sided valleys of the upper waters would provide less abundant food for the aborigines than would the mature, broad valley lands of the lower river. These points involve research for the future and are of no further concern here. The available evidence validates the exclusion of the Murray and Darling River tribes from the basic series on the grounds that unearned surface waters markedly alter their area ratios and hence density ratios.

INSULAR POPULATIONS

Insular tribes represent another category in which deviations from a primarily terrestrial economy are a cause for disqualification. On *a priori* grounds all tribes residing completely or partially on islands were excluded from the total series, and hence from the basic series. This decision was based on several factors. The very configuration of islands, with a long coastline enclosing a relatively small area of land, indicates that abundant marine foods should be available. Further, unlike mainland tribes, the area of land available to a given tribal population is determined by variations in the topography of land and eustatic sea level rather than by a complex of social interactions between groups of people. Thus the area

of islands bears no functional relationship to our assumed constant of 500 persons per tribe, save in the cases of islands large enough to support a greater population than this, or so close to the mainland that a single tribal population can maintain an adequate level of internal cohesion across the straits. An insular environment may operate both to increase aboriginal densities as compared to terrestrial standards, or to limit the size of a population in the case of very small islands lying well offshore. Both factors may be operative in many cases.

Despite these complexities, it is of some interest to compare the position of the insular tribes with the basic series. In figure 5 the positions of 13 tribes wholly insular are plotted with solid circles, and 5 tribes occupying islands and portions of the adjacent mainland are shown by half-solid circular symbols. In the latter cases the islands provide from 20 to 65 per cent of their total domain. Data for nine additional tribes even less insular in nature are given in table 1. The plotted positions for the tribes in the first two categories show the expected deviations from the basic curve in the direction of higher density ratios. A single exception, the Tiwi tribe of Melville and Bathurst Islands, has a much larger population than the assumed constant of 500 persons, and this may partially explain its position above the curve.

Table 1 presents an interesting trend in terms of insular density ratios. The total series of 27 wholly or partially insular tribes have a mean density ratio of 2.49, and if the Tiwi are omitted, the ratio rises to 3.07. For 13 completely insular tribes, the density ratio is 2.86, a value which rises to 5.58 with the exclusion of the Tiwi. Five tribes whose domain is from 65 to 20 per cent insular show a mean density ratio of 4.56. Eight tribes with 10 per cent or less of their territory on islands show a mean density ratio of but 1.53. Despite the small size of these samples, and the ecological variations along the different coastal regions of Australia, it is perhaps fair to infer that marine food resources do importantly alter aboriginal ecology and hence density. The detectable trend for density ratios to increase in passing from slightly to completely insular tribes is taken as confirmation, even though changes in population size may also be involved. As mentioned earlier, tribes with a foothold on the mainland have potential room for expansion to our assumed constant of 500 individuals per tribe via give and take adjustments with neighboring peoples, but totally insular groups may have their numbers limited in part by available land area. Despite their limitations the data do justify the decision to eliminate on ecological grounds both completely and partially insular tribes from the total and the basic series.

THE COASTAL POPULATIONS

The ecological position of the mainland coastal tribes is one further aspect of the problem posed by the addition of marine foods to the aboriginal diet. The available data consist of 119 tribes totally unselected, save that four gaps occur along the northern coast as shown in figure 1. The average

area ratio for the series of coastal tribes is 0.751 and the mean density ratio reaches 1.33. On a gross level access to the coast may be interpreted as increasing density by one third over the value predicted for inland tribes by the basic rainfall equation. Thus the systematic exclusion of the coastal tribes from the basic series seems justified, since there is no evidence to suggest that their tribal populations are smaller in numbers than that assumed for the whole continent.

But a regional examination of the coastal tribes indicates a complex pattern of variation which implies that much is yet to be learned of their ecology at a detailed and local level. It is convenient to survey briefly these tribes, beginning at Eyre Peninsula and going around the continent in a clockwise direction, lumping together groups of tribes which show generally consistent deviations from predicted density ratios. The 119 tribes have thus been divided into 12 subgroups which are listed in table 1 under the subheading, I-C. The first local group, C-2, extends from the Eyre Peninsula westward across the shores of the Great Australian Bight, around Cape Leeuwin to Geographe Bay. This group is characterized by the surprisingly low density ratio of 0.70. For the tribes along the Bight this low ratio may be explained by the total lack of even transient streams, the limiting factor of very scarce surface water in the form of springs and soaks, and a lack of watercraft. But it is more difficult to account for the continuance of these low density ratios into the well-watered southwestern corner of the continent. A detailed study of the marine fauna might provide a partial answer.

The second group of tribes, C-3, extends northward from Geographe Bay around Northwest Cape to Nickol Bay and shows the inexplicably high mean density ratio of 2.21. This coast has low rainfall and intermittent streams and rivers. At first sight it would seem to offer few advantages for aboriginal life. Yet Grey (1841), traversing much of this coast on foot under forced marches, concluded that parts of this region were the most densely settled he had seen in aboriginal Australia. He noted valleys rich in yams and lagoons abundant in their marine life and waterfowl. Further, marine turtles extend as far south as Shark Bay, so that this coastal country may have been more attractive from the native point of view than rainfall values suggest.

The next group, C-4, consisting of but two tribes along the Eighty Mile Beach, shows a mean density of 1.61, which reduction may be accounted for by the poor country and lack of streams. A fourth group, C-5, consisting of tribes along the Dampier Land coast, shows a mean density ratio of 5.44, the highest value for any of the coastal regions. Unless an abundance of turtle and dugong make this an ecologically rich coast, it may be suspected that the size of the tribal populations here falls below our assumed constant, and results in an apparent increase in the density ratio. Neither aboriginal food resources nor population estimates are obtainable in detail to determine this point.

There are at present no data for the tribes of the Kimberley coast, so that the next group, C-6, consists of scattered tribes along the coast of Arnhem Land. Here the mean density ratio falls to a more normal value of 2.45 which may be more representative of the tropical coastal regions. After a short break, group C-7, lying along the lowland stretch of the southern shore of the Gulf of Carpentaria, shows a mean density ratio of 1.12, a value which needs explanation in terms of both local ecology and population sizes. After another break and beginning at the tip of Cape York Peninsula a block of 15 coastal tribes extend down to the northern margin of the rainforest. They comprise group C-8 and show a mean density ratio of 1.71. Some of these tribes are essentially marine rather than terrestrial in their mode of life, owing to the dugout canoe, a trait diffused from New Guinea, which allows increased efficiency in the exploitation of marine foods.

Group C-9 includes eight rainforest tribes with a mean density ratio of 0.96, a value slightly below that predicted for inland tribes having no access to the sea. A breakdown of this group reveals that the four northern members, all of whom use the dugout canoe, have a mean density ratio of 1.63, whereas the four southern tribes, limited to less efficient watercraft, average but 0.76 for their density ratio. It would be tempting to consider that these differences in density ratio are a measure of the ecological contribution of the dugout, but present data are insufficient to allow this conclusion. With more information it may be possible to evaluate the contribution made by this cultural factor to the ecology of a coastal people for whom turtle, dugong and other marine foods are of great importance.

The tribes of the central Queensland coast, C-10, show the inexplicably low mean density ratio of 0.79. Since this region is well watered, with permanent rivers, and both terrestrial and marine foods are abundant, one is at a loss to explain the low density ratio in ecological terms. It may be that this value reflects a systematic increase in population size; present data suggest but do not allow this as a final decision. The next group, C-11, roughly extends from Brisbane to a little north of Sydney and yields a mean density ratio of 0.95. This low value may reflect the disappearance of turtle and dugong along the coast in combination with mountains which in many places approach the sea and may reduce the exploitable terrestrial resources. Another group, C-12, stretches from just north of Sydney to a little east of Melbourne and gives a mean density ratio of 1.65. Here again mountains encroach upon the sea, but the coast is broken by numerous deep bays, estuaries and lake-like lagoons which, through their lengthened shoreline and ecological variation, probably confer advantages not to be predicted from mean annual rainfall as the sole determinant of density. On the other hand, early population estimates (Kryzwicki, 1934) suggests that here the size of the tribal population falls below the assumed value of 500 persons, and thus may cause an apparent increase in the density ratios. The relative contributions of these two factors cannot yet be determined.

The final group, C-13, extending from Melbourne through to Yorke Peninsula, and including the coastal tribes at the mouth of the Murray River shows an average density ratio of 1.65. This value is of little significance because of the ecologically heterogeneous nature of the tribes which contribute to it.

The foregoing rapid survey of the regional variations in the average density ratios among Australian coastal tribes provides but few useful generalizations. As might have been anticipated from the relative contribution of marine foods, the coastal tribes have density ratios intermediate between the insular and purely terrestrial inland tribes. Beyond that, it seems safe to infer that density ratios run higher along tropical than temperate coasts. Here the sea turtle, and to a lesser extent the dugong, may contribute importantly to the difference. Evidence from the Bight indicates that a lack of free surface water may act as a limiting factor of even coastal peoples. There are hints that technological improvements, such as the dugout canoe, may measurably influence the extractive efficiency of a people in a given environment, and hence directly change their density. It is quite evident that the ecology of coastal peoples becomes sufficiently complex so that most of the observed variations cannot be explained in terms of rainfall alone.

A detailed ecological investigation of the coastal tribes cannot be undertaken at this time, but certain of the steps necessary for a solution can be predicted. Systematic deviations in the size of tribal populations, if they occur, must be determined. The relative contributions of marine and terrestrial food resources must be evaluated, for rainfall will be of predictive use only for the latter. Further, there are some cultural hints that coastal peoples do not exploit the available terrestrial foods as intensively as do interior tribes. Along the rugged southeastern coast the encroachment of mountains will require corrective factors for differences in altitude and land gradients, for these will affect the types of land resources available and the intensity with which they can be exploited. Finally, the ecology of the marine contributions must be defined in detail. Differences between cold and warm water biota must be established. The contribution per running mile of deep water shorelines, sandy shoal water, brackish bay and lagoon, and mangrove swamp will require determination for different sections of the coastline. The task is a formidable one, but some predictive formulae, although clearly complex ones, can be derived to take the more important variables into account. Such an analysis would be facilitated if ethnologists, who have provided much useful qualitative information, would go further and obtain quantified data concerning the important foods used in a full seasonal cycle.

POPULATIONS EXCLUDED ON CULTURAL GROUNDS

The preceding sections validated the exclusion of categories of tribes which for ecological reasons had densities deviating from those predictable from the basic rainfall equation. There remain two cultural factors to be

justified as grounds for elimination. Since they operate to change the size of the tribal population, it will be convenient to use the area ratios for comparison. The first factor concerns the influence of a more advanced type of political organization characterized by matrilineal descent. The three excluded tribes, the Wiradjuri, Kamilaroi and Wongaibon, showed area ratios of 8.46, 5.03 and 2.10 respectively. The three tribes together show a mean area ratio of 5.02. It may be inferred from this that tribal populations in this region approximated 2,500 persons, as against the value of 500 assumed for the continent. The early observers quoted by Kryzwicki (1934) gave even higher estimates for the first two tribes. Thus it may be concluded that these three tribes on cultural grounds should not be included in the basic series.

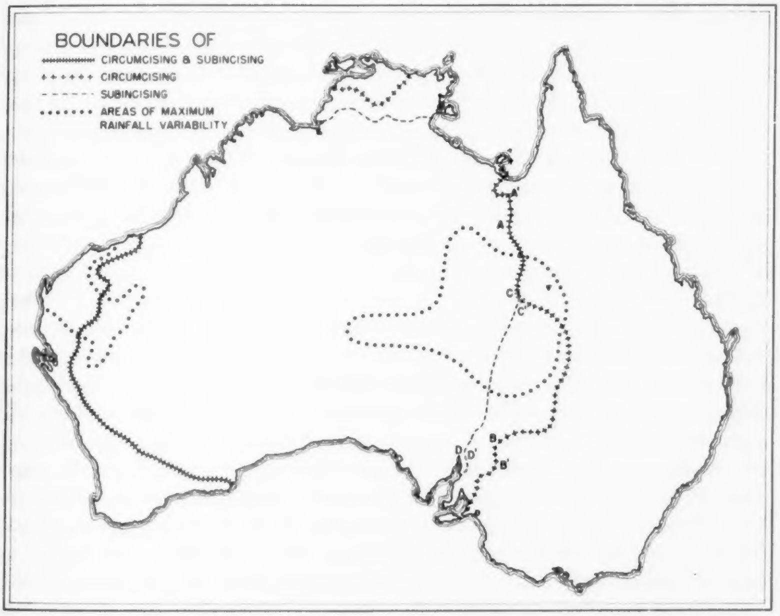

FIGURE 7. Boundaries of circumcision and subincision initiation rites.

A second cultural factor considered as a basis for exclusion in the basic series is involved in the spread of the initiation rites of circumcision and subincision. These ceremonies seem, in terms of age-area theory, to have originated in the center of the continent, and hence at the outer boundaries of their distribution they appear to be recent acquisitions among the affected tribes. The distribution of the rites are given in figure 7, in which an eastern, a northern, and a western set of boundaries can be identified. On its eastern limits, the boundaries of the two ceremonies coincide from the Gulf of Carpentaria southwards until a point of bifurcation is reached;

then the limits of circumcision pass in a more easterly direction to ultimately reach the Gulf of St. Vincent, while the boundary for subincision proceeds in a more westerly direction to terminate at the head of Spencer's Gulf. This eastern set of boundaries shows the phenomenon of fragmentation most clearly since larger numbers of tribes are available along its limits, and coastal ecological disturbances are minimized. It is our thesis that the recent acquisition of either or both of these initiation rites operates in some as yet unknown fashion to produce tribal units with fewer than the 500 persons assumed as our continental constant. In short, the advent of these ceremonies is associated with tribal fragmentation.

This hypothesis may be tested by comparing area ratios and early population estimates. As shown in table 1 subheading 2-B, the 25 tribes lying just west of the circumcision line have an average area ratio of 0.467, whereas the 21 tribes adjacent to the line on the east show a mean area ratio of 0.728. Thus as predicted from the basic rainfall equation, tribes lacking the circumcision ceremony have an area 1.56 times as large on the average as those tribes which have recently received the rite. The contrast would be even greater save for the fact that the coastal tribes do not follow this pattern as closely as do the interior tribes. A better basis for comparison can be obtained by eliminating the aberrant coastal tribes. When this is done, a transect of 17 non-coastal tribes lying between points A-B to the west of the circumcision line shows a mean area ratio of 0.286, whereas 13 tribes comparably situated to the east of the boundary have an average area ratio of 1.002. By this comparison, the unaffected tribes average 3.50 times the area of those which have newly taken over the rite. In figure 5, these 13 unaffected tribes are plotted as hollow squares, and it will be seen that they are distributed rather uniformly about the basic rainfall curve. The corresponding 17 affected tribes are plotted as crosses, and they consistently fall far below area values predicted from rainfall, thus demonstrating reduced tribal areas. A further disturbing factor arises from the presence of ecologically important unearned surface water from the Darling River in the territory of nine unaffected tribes lying to the east of the line. By further eliminating the tribes thus influenced, and their partners in comparison across the line, even more striking results are obtained. Thus 12 affected tribes west of the line show a mean area ratio of 0.318, whereas eight contiguous tribes to the east of the line give an average area ratio of 1.33. Even though the smaller numbers involved diminish the validity of the comparison, it is striking that the non-circumcising tribes have areas averaging 4.19 times larger than their western neighbors who have recently acquired the ceremony. This series of comparisons suggest that, in the absence of visible ecological factors capable of producing changes in densities, the tribes just to the west of the line are characterized by much smaller population sizes than the assumed constant of 500 persons. The population estimates for this region as summarized by Kryzwicki (1934) strikingly confirm this inference. There can be little doubt

that the diffusion of circumcision rites to the east has been associated with tribal fragmentation.

The above analysis was concerned with the rite of circumcision, either alone or combined with subincision. Since the most striking differences were found in a transect in which some of the affected tribes practiced subincision as well as circumcision, it will be of some interest to examine the effect of subincision alone as a differentiating trait. This can be achieved by comparing tribes just to the west of the subincision line, as shown between points C–D in figure 7, with corresponding tribes practicing only circumcision lying just east of this boundary between points C′–D′. The six affected tribes to the west of the line have a mean area ratio of 0.185, whereas the five unaffected tribes across the line to the east show an average area ratio of 0.262. The tribes which practice only circumcision have 1.42 times as large an area on the average as those neighboring groups which perform both initiation rites. Despite the very small size of the samples involved, these data suggest that the rite of subincision when recently acquired tends to produce tribal fragmentation beyond that involved with the spread of circumcision alone. The available estimates given by Kryzwicki (1934) indicate very small tribal populations for the tribes here practicing dual initiation rites, and thus lend confirmatory evidence to the theory of fragmentation.

The evidence from the northern boundaries of circumcision and subincision is based upon very small samples, but it tends to substantiate the trends observed among the tribes along the eastern limits of the rites. Three non-coastal tribes lying just north of the circumcision boundary show an area ratio averaging 2.31. Five interior tribes positioned between the limits of circumcising and subincising show a mean area ratio of 1.56. It should be recalled that the Daly River tribes and the Murngin complex of northeastern Arnhem Land, both coastal in location and lying between these lines, were remarked by Tindale (1940, p. 150) as showing fragmentation. Three interior tribes just inside the subincision boundary average 1.01 for their area ratio. These data are scanty but consistent with the suggestion of fragmentation following the acceptance of both circumcision and subincision that was noted along the eastern limits of these ceremonies.

The western boundaries of the rites coincide throughout their length. An examination of the area ratios on either side of this line does not confirm the trends found for the eastern and northern boundaries. The 19 unaffected tribes to the west of the line show an average area ratio of 0.534, whereas the 12 tribes practicing both rites just east of the line have a mean area ratio of 0.751. There are several local factors which may explain these discordant results. Information relating to the tribal groups in this region is less detailed than for most of the rest of the area used for analysis. Thus occasionally subtribal units may have been confused with tribal entities. The boundaries of most tribes are approximate rather than fully defined by the data. As noted earlier coastal tribes do not closely follow the pattern of fragmentation established for interior tribes: of the 19

tribes outside the boundary, no less than 11 are coastal in location. Further, this coastal stretch was characterized by unexpectedly low average area ratios. Unfortunately there are virtually no population estimates for these tribes to indicate whether their populations conform reasonably to the assumed constant of 500 persons.

Finally, a further environmental factor may have some influence here. The two areas of maximum rainfall variability in Australia, occur (modified after Gentilli, 1946), as might be expected, in arid regions. The largest is found centered in the Boulia region of Queensland, as shown in figure 7. Here the pattern of tribal fragmentation so closely follows the region affected by minimum rainfall reliability as to suggest that some causal relationship exists between the two. In these terms unreliable rainfall may increase the tendency toward fragmentation which also seems associated with the recent acquisition of circumcision and subincision. A second area of maximum rainfall variability centers in Western Australia along the Ashburton River, as indicated in figure 7, and extends over the broken highlands of the Hammersley Range to the north and the Barlee Range to the south. Again, maximum fragmentation seems to have coincided remarkably with the pattern of minimum rainfall reliability. For these various reasons it is considered that the negative evidence from the western boundaries of the initiatory rites does not vitiate the earlier conclusion that tribes which have recently acquired circumcision and subincision rites show a tendency toward fragmentation. The affected belts of tribes have therefore been properly excluded from the basic series.

TRIBAL FRAGMENTATION

The question as to why such fragmentation should occur is not to be easily answered. The spread of both initiation ceremonies is known to have been a gradual and essentially undramatic process. Neighbors were known to be practicing the rites, they were witnessed by visitors, and when introduced later with ceremonial sanctions, it is difficult to comprehend why diffusion should be accompanied by social shock-effects. The problem is further complicated by the fact that both the patterning of area ratios and the population estimates of early observers for tribes deep within the affected area strongly suggest that tendency toward fragmentation was transient, that tribes which had practiced the rites for longer periods of time tended toward reintegration so that tribal populations returned to the assumed constant of about 500 persons. It is on these grounds that a block of 20 tribes in the center of the area of initiating tribes have been included in the basic series. It is perhaps enough to indicate here that the area ratio method has served to identify the phenomenon of transient tribal fragmentation in Australia, to associate it with the diffusion of circumcision and subincision, and to note that the tendency seems heightened in areas of minimum rainfall reliability. The functional explanation will certainly be found in the realm of social forces and interactions, and thus will await further research by cultural anthropologists.

AVERAGE SIZE OF TRIBES

Throughout the discussion the assumption has been used that the Australian tribe, in a broad statistical sense averages about 500 persons. In this assumption the existence of a marked central tendency is more important than the absolute size of the estimate. The calculations of Brown (1930), who systematically surveyed the problem, yield averages from 437 to above 523 persons per tribe. Kryzwicki (1934) comprehensively covered the available literature and reached similar values. He tabulated early estimates for 123 tribes with the following results: 70 tribes numbered less than 500 persons; 37 tribes numbered between 500 and 1,000; 12 tribes ranged between 1,000 and 2,500; and four tribes contained more than 2,500 individuals. From these figures Kryzwicki concluded that the tribe in Australia averaged about 550 persons, but he cautioned that his compilation contained inherent errors. The majority of his estimates originated from the correspondents of E. M. Curr, and Kryzwicki (1934, p. 305) provided the following evaluation of them:

> ... individuals, with but few exceptions, who were fundamentally far from any systematic scientific interest in the phenomena observed by them. In the best cases they were persons who were willing to relate what they had seen during their personal contacts with the natives. They saw, or rather encountered, a certain number of bands forming integral parts of tribes: this was usually enough for them, and more often than not they treated such bands as tribal communities.... And so, more especially as regards tribes with a population of under 500 souls, the possibility is very great that we may have included in our list such names which are designations of portions of tribes.... Another difficulty to overcome is to ascertain where the limits of a tribe end and those of a nation begin. The category of tribes with over 2,500 head of population quoted in our table really embraces only nations.... We cannot issue any definite opinion whether these were really nations or only large tribes, on the basis of the material we have at hand. But we draw attention to this difficulty as also to the caution which is indicated and even essential when studying the data given hereunder.

Kryzwicki further warns that his list of 123 tribes represent poor regional sampling for the continent, and that Curr's informants tended to ignore the many small tribes, reporting on disproportionate numbers of large and very large tribes. He concludes cautiously that the typical population of an Australian tribe may be considered to range between 300 and 600 persons.

Of the 123 tribes listed by Kryzwicki it has been possible to identify 77 as corresponding to those defined by Tindale (1940). Most of the unidentified "tribes" are hordes by the latter's list, some cannot be equated with Tindale's nomenclature, and half a dozen required exclusion for other reasons. Although Kryzwicki was fully aware of the dubious accuracy of the estimates he quotes, the situation is further complicated by an epidemic which seems to have been smallpox, that spread through parts of eastern Australia in the early nineteenth century, and may have affected most of the continent. Depopulation clearly followed, but the magnitude of its impact cannot now be estimated. This factor may result in Kryzwicki's values, and our own, being underestimations.

COMPARISONS OF POPULATION ESTIMATES

Despite these difficulties it seems worth testing population data against our predictions for tribal population size derived from the basic rainfall equation. The method of estimating the size of tribal populations from the area ratio determined from the basic equation requires that the size of the populations approximates a statistical constant. In this case it has been assumed to be 500 individuals, but should later more accurate data indicate a changed value, it would not affect the method. Estimated population size will vary directly with the area ratio: thus an area ratio of 1.00 indicates a tribal population estimate of 500 persons; a ratio of 2.00 gives an estimate of 1,000; and a ratio of 0.50 an estimate of 250 persons. Since the method is applicable only to those groups of tribes in which the area is a direct and constant expression of population size, the following categories in which ecological factors modify tribal densities have been eliminated: (1) coastal and insular tribes; (2) tribes affected by unearned surface water.[5] This leaves for comparative purposes the basic series plus those circumcising and subincising tribes which have not been excluded by the above criteria. From Kryzwicki's list of tribes there are 45 which fulfill the necessary conditions. Figure 8 shows the population estimates of early observers plotted against estimates calculated from area ratios. Prior to plotting, the estimates by field observers were independently graded as to their validity as judged from cultural factors involving care of observation and internal consistency. Of the 45 estimates, 11 were judged as good (largely the data of modern anthropologists), 27 were considered as fair, and 7 were classed as poor in probable accuracy. These categories are shown by appropriate symbols in figure 8. It will be noted that the estimates considered to be poor give the greatest scattering, whereas those thought to be good give the least, thus suggesting that the independent judgments of the accuracy of these estimates was made with a basis of reason.

The relationship between the observer's estimates of population size and the values predicted by the area ratio methodology can be tested in several different ways. One involves the coefficient of linear correlation, r, and merely gives the degree of association. The value for r is 0.436 for the total series of 45 tribes, and 0.509 for the 38 tribes judged to represent good or fair estimates. In view of the scattering shown by the 7 estimates judged to be poor, it seems proper to ignore this category as representing inaccurate guesses by poorly qualified observers.

A better method of measuring the agreement between the two sets of estimates is given by r_1, the coefficient of intra-class correlation. This more exact way measures the deviation of the data from exact agreement, represented by the dotted line. Its calculation involves the duplication

[5]The three large "confederacies" have been excluded to keep the coordinates of the diagram shown in fig. 8 within reasonable and convenient scale values. They should perhaps also be excluded as being probably affected by unearned surface water.

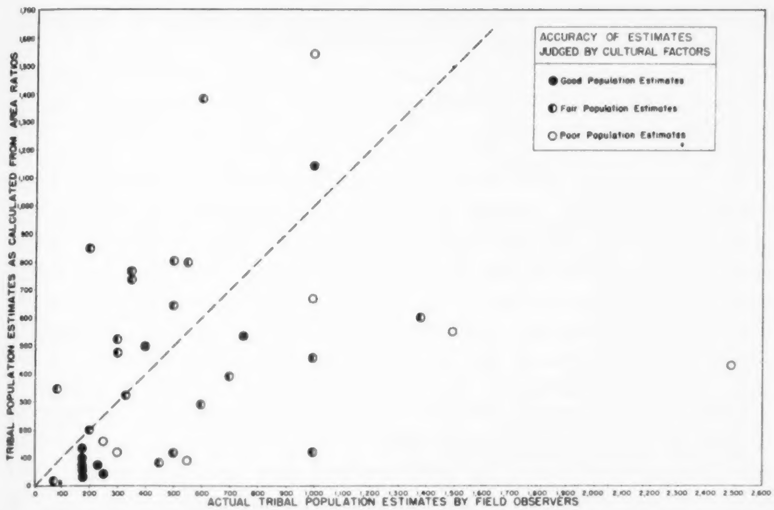

FIGURE 8. Correlation between tribal population estimates from early observers and those calculated by area ratio methodology.

of the data by reflection about this axis of agreement. The value for r_1 for 45 tribes is 0.400; for the 38 tribes judged to represent good to fair estimates it rises to 0.504. Although not high, the degree of agreement indicated is fairly satisfactory considering the dubious nature of the tribal estimates by early observers. With accurate estimates from modern observers and a refined predictive equation, a much closer measure of agreement should result. Even in its present form the result suggests that the assumption of 500 persons per tribe is close to a proper figure. More im-

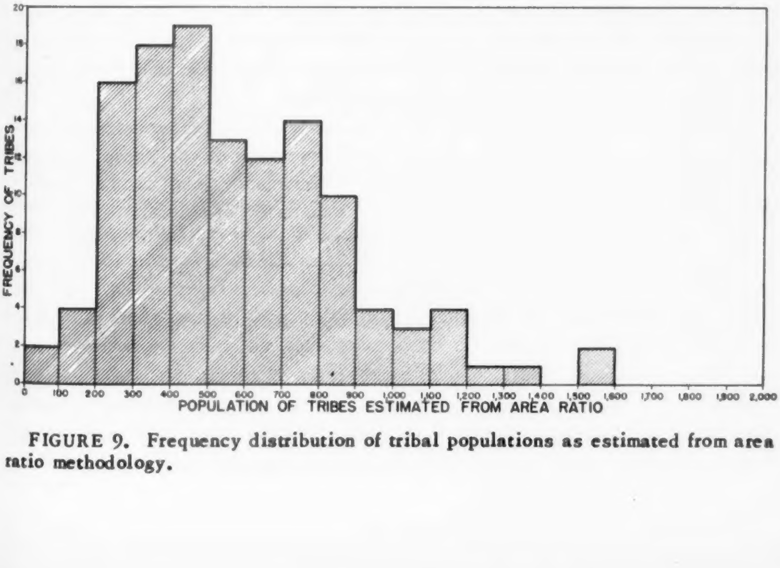

FIGURE 9. Frequency distribution of tribal populations as estimated from area ratio methodology.

portantly, the result validates the area ratio methodology, and suggests that when the basic equation has been refined to include the full set of ecological variables it will become more accurate than the population estimates quoted by Kryzwicki, and hence a useful demographic instrument for aboriginal Australia.

VARIATION IN POPULATION SIZE

If it will be granted that the validity of the assumed average of 500 persons per tribe has been demonstrated as a statistical abstraction, it becomes feasible to investigate the variance of the size of Australian tribal populations. Estimates for the 123 tribes of the basic series were made from their area ratios and the results were seriated. Using group intervals of 100, the distribution is shown in figure 9. It will be noted that the frequencies for the extremes of the distribution seem to show a deficiency in numbers. Thus of the 123 tribes, but 6 cases fall below 200 and only 15 occur in the unlimited range above 900. Consequently there appears to be a more than expected clustering tendency for tribes to average between 200 and 900 in population. It is unfortunate that the total series is too small in numbers to allow a statistical demonstration of the significance of this clumping. The mean value of the frequency distribution lies at 575, but this value is an artefact resulting from the use of arithmetic mean rather than the geometric mean. (The proper calculation was precluded by limitations of time in preparing for two years' further field work in Australia.) Thus the calculated mean is higher than the true mean, which by the nature of the area-ratio method is dependent upon the value assumed for the size of the tribal population and should have approximated 500. The mode falls between 400 and 500, giving a measure of the skewness of the distribution. The standard deviation is 300, and since it would presumably be of the same general magnitude for the proper calculation using the geometric mean, the corrected values can be estimated as a mean of 500 with a range from 200 to 800 as defined by plus and minus one standard deviation. Despite the evident inadequacies of the data, it may be claimed that Kryzwicki's earlier analysis is essentially confirmed.

The validation of 500 persons per tribe as a statistical constant of approximately correct magnitude allows the conversion of the basic equation expressing the relationship between tribal area and mean annual rainfall into a new form expressing density, D, as a function of rainfall:

$$D = \frac{0.0703037}{X^{-1.58451}}$$

where X is mean annual rainfall, (as indicated in figure 4).

DISCUSSION

In the early stages of this investigation it was assumed, in the absence of adequate data for the size of the Australian tribal population, that in the basic series the size of the tribal territory is an inverse measure of the

density of the population, through the interlocking assumption that there tribes average about 500 persons in size. The high degree of curvilinear correlation between mean annual rainfall and the size of the tribal area confirms both of the intervening assumptions. The lack of functional validity in either case would have resulted in a low value for rho, save for the improbable instance in which one unrelated assumption somehow systematically compensated for the uncorrelated vagaries in the other. The value of 0.81 for rho is ample evidence that both of these independent assumptions hold true with a reasonable degree of validity.

A brief examination of the variance of the size of tribal populations in this correlation is revealing. With rho equal to 0.81, the explained variance of the dependent variable amounts to 65 per cent of the total, the unexplained variance to but 35 per cent. It is understood that the explained variance is expressed not only in terms of mean annual rainfall, but also in terms of such other variables as may prove to be partially correlated with the former. The unexplained variance must be considered to contain deviations due to the following types of errors which diminish the value of rho:

(1) *Errors of verification:* the nature of the tribe as an entity; location of tribal boundaries; instrumental errors in planimeter values for tribal areas; type of map projection; assignment of mean annual rainfall values tribally; and unrecorded microgeographical variations in rainfall.

(2) *Errors of space:* assumption that basic series ecologically represents complete regional homogeneity.

(3) *Errors of time:* assumption that no shifts in rainfall values through time have affected recorded tribal boundaries.

(4) *Errors of culture:* assumption that with broad cultural uniformity in Australia no small regional differences exist which might affect extractive efficiency.

(5) *Errors of the environment:* use of mean annual rainfall as the sole environmental variable. It must be expected that the following variables will also influence aboriginal densities; (a) rainfall reliability, (b) rainfall intensity, (c) seasonality of rainfall, (d) humidity, (e) evaporation rates, (f) temperature, (g) length of growing season, (h) altitudinal differences, (i) soil variations including trace mineral deficiencies, and (j) other unspecified factors affecting the biota.

(6) *Errors in population size:* appreciable deviations from assumption that tribal populations approximate 500 persons as a constant will occur, whether systematic or erratic in nature.

In addition to the above specified sources of error, the value of rho is dependent upon the causal relationship between mean annual rainfall and size of the tribal population. The exact contribution to the unexplained variance can be evaluated for none of these types of errors, but each of the first four categories must have affected it slightly, while the last two must have increased it substantially. Thus it must be inferred that a very close causal relationship exists between rainfall and the size of tribal territory; that the densities of Australian aboriginal tribes are rigorously subject to environmental determinism.

Anthropologists have been so impressed with the bewildering variability of cultural expression that they have tended to deny the possible operation

of environmental determinism. Historically this is understandable, for the early proponents of the latter concept claimed so much that their position was easily discredited. Our claim here is merely that on the simplest cultural levels the densities of human populations are primarily determined by the variables of the environment. Since man, like other living things, must extract his energy from the environment there are good ecological reasons for such determinism. In economies higher than the hunting and collecting level, the environmental control of densities will become less rigorous and hence less visible. The same will be true for cultures changing their form rapidly in time, especially at the technological level. But as long as man extracts his energy from the environment by crude means his population density will depend to some extent upon such determinism. For man in the Pleistocene, and much of our evolutionary interest in him centers in this period, the environment must have determined his population density as completely as it did for the Australian aborigines.

It follows as an important corollary of environmental determinism of aboriginal densities that these populations must have been in essential equilibrium with their environment. This idea will not be new to biological students of natural populations, for it is a major premise in the structure of evolutionary thinking, but it has remained foreign to most anthropological conceptualization. Although utilized in a qualitative form, either explicitly or implicitly, by Kaberry (1939), Kryzwicki (1934), Steward (1938), Tindale (1940), and Wolfe (1933) among others, it has not received widespread anthropological acceptance. It is not claiming too much to insist that studies of the population dynamics of man at a hunting and collecting level of economy, whether Pleistocene or modern, must start with the premise that such groups are usually in equilibrium with their environment.[6] A more detailed discussion of the utility of this concept will be found in Bartholomew and Birdsell (ms.).

The present study has a number of applications to research in aboriginal Australia. The finding that the size of the tribe approximates 500 persons in a statistical sense validates one of the primary simplifying assumptions used by Birdsell (1950) for the construction of simple gene flow models used in exploring the dynamics of aboriginal populations. Even in the present tentative form of the basic equation, the area ratio method allows for the construction of considerably improved gene flow models compared to those previously published. In the latter devices such as "accelorators" were used in the Boulia region, and "inhibitors" in the region of the New South Wales "confederacies," to partially adjust for suspected deviations from the tribal norms. It is now evident that these adjustments were much too conservative and that other regions may need alteration. It

[6]Exceptions occur among such peoples as the salmon fishermen of the Northwest Coast and the bison hunting horsemen of the Great Plains of North America. Technically both belong with the hunting and gathering peoples but in each case these more complicated cultures are based upon special circumstances. Among culturally simple groups the concept should hold with considerable regularity.

is now possible to start with Tindale's tribal map and to make the corrections required for those areas in which the average size of the tribal population systematically deviates from the statistical mean of 500 persons. Sporadic deviations from this mean may also be corrected by the area-ratio method. Thus an idealized grid of genetic isolates can be created for modern aboriginal Australia which is superior for gene-flow models to the actual tribal map.

In a like way the high correlation between mean annual rainfall and the size of the tribal area will allow the construction of idealized genetic isolate grids for any time point in the Recent or terminal Pleistocene for which paleoclimatological estimates for approximate rainfall can be provided. Such data now are too scanty to be used, but recent strides in the natural sciences in Australia suggest that they may become available within the next decade. Then it will be possible to construct gene flow models, to determine the distribution of aboriginal densities, and to take an approximate census for a given period of prehistory. When the paleoclimatological variables can be defined for the now sunken Sahul Shelf, which formerly connected Australia with New Guinea during glacial periods of eustatic lowering of sea-level, the same techniques can be applied to that submerged land surface, an area which is of some importance in the reconstruction of population dynamics in prehistoric Australia.

The basic curve in figure 4, which depicts the relationship between mean annual rainfall and the size of the tribal territory, suggests that the apparently simple material culture of the aborigines is in fact surprisingly adaptable. While the curve is a statistical artefact, the data show a remarkable smoothness in their distribution around the curve from one extremity to the other. This may be interpreted as indicating that, despite the relative uniformity of their material culture throughout the continent, the aborigines maintain the same high level of extractive efficiency (for a hunting and collecting people) from the most arid environment to the wettest regions in Australia. Thus no breaks occur in the distributional pattern of the data as one passes from spinifex and sandhill country at one extreme through the various types of desert scrub lands, mallee country, grassland and open forest, dense eucalyptus forest, finally to the nearly impenetrable rainforests of the Cairns tableland region. Both the flora and fauna change drastically in abundance and in type in such a transect and the pattern of the data is witness to the constant level of cultural adaptedness of the aborigines. One qualifying statement must be made at this point. If densities were substituted for the size of tribal areas in relationship to rainfall, the picture might change slightly. This conversion is dependent upon the absence of systematic regional variations in the average size of the tribal population.[7]

[7]As stated earlier, there is little evidence for such variation save possibly in the region of the tropical rainforest. Tindale informs me that an examination of his geneologies for the tribes of this region suggests that the nuclear 11 tribes may have had considerably smaller populations than the 500 considered generally valid

The broad generalizations resulting from this investigation are applicable to other culturally simple hunting and collecting peoples in different places and in different times. But it must be stressed that the specific variables and the detailed constants for the Australian equation are not transferable to any other people. The equation relating human population densities to a given environment will depend in each instance upon three major categories of variables:

(1) The variables of the environment in terms of climatic, soil, and topographic factors;

(2) The variables influencing the phylogenetic history of the local biota;

(3) The variables in culture which determine a people's extractive efficiency.

In Australia mean annual rainfall at this preliminary level of analysis gives reasonably accurate predictions for population densities, and the same may hold true for other interior temperate and tropical populations. On the other hand, a people such as the Eskimo living in the Arctic would show densities conditioned by other variables such as temperature, length of the growing season, and the various factors which affect the marine fauna upon which they are dependent for winter survival. In general those variables which influence the local biota most importantly can be expected to be the ecologically important variables of the density equation.[8]

Even regions which seem environmentally to be approximately equivalent to portions of Australia will not show similar human densities or density equations for peoples at about the same level of extractive efficiency. The Shoshoni of the Great Basin in the United States, and the Bushmen of the Kalahari Desert of South Africa have been shown by Vorkapich (ms.) to have quite different densities from the Australians for the same rainfall regimes. Aschmann (ms.) shows even more striking density differences for the hunters and collectors of the middle region of Baja California. With similar environments, and extractive efficiency differing but little among these four peoples, the disparities in their densities must be attributed primarily to differences in the local biota and food chains. The Australians are dependent upon a unique flora and a marsupial fauna. The trophic levels these comprise will not be duplicated elsewhere. The Shoshoni have specialized of necessity as seed and root gatherers; game is of but

for the continent. If confirmed, the curve for density would deviate in form from that shown in fig. 8, in that a point of inflection would occur at about 60 inches of rainfall, and beyond this value densities would again diminish. This change would not greatly modify preceding discussions, but it would require curve fitting anew, and a different mathematical expression for the relationship between density and rainfall.

[8]While the Australian data lent themselves to an analysis primarily based upon the size of tribal territories, it must not be presumed that the relative constancy of size of the Australian tribal population will be met with among all other peoples. In terms of cultural analogy, the assumption of similar sized population groups in the Pleistocene makes an attractive working hypothesis, but among modern peoples it seems likely that similar investigations will have to deal directly with data for densities.

little importance to them. The Bushman can depend more upon grazing animals which are more abundant in his environment than in those of the other three peoples. For Baja California human densities were markedly conditioned by the presence of a wealth of starchy plant food in the form of half a dozen species of agave. These brief examples are sufficient to indicate that the phylogenetic history of the local biota of a region is of prime importance in the formulation of the human density equation; constants derived from one region cannot be applied to another biotic province. The fact that the Indians of middle Baja California with lower rainfall and no higher extractive efficiency show more than 50 times the density that Australians do in roughly equivalent climatic conditions highlights the importance of the biotic variable. Its evaluation will require detailed and quantitative ecological research upon the composition of food chains and trophic levels as they affect man.

The efficiency with which a people extract energy from their environment will vary with the content and complexity of their culture. Forms of social organization may contribute to efficiency, but for simple hunting and collecting cultures the techniques for the fabrication of primary and secondary tools will usually be of greater importance. It is unfortunate that to this late date ethnologists have provided little quantitative data on the relative efficiency of extractive devices used at this cultural level. Without such information, and there remains but little time in which to collect it, it will remain impossible for archeologists to evaluate the extractive efficiency of the various populations in the Pleistocene which are necessary to our understanding of human evolution. In view of the magnitude of the task remaining to be accomplished in this field it is perhaps fortunate that of the three categories of variables influencing the human density equation that referring to cultural variation appears to be the least important. For most simple hunting and collecting peoples, a surprisingly large proportion of the total food supply is probably obtained through the use of the unaided hands, a digging stick, and the simple spear or bow.

SUMMARY AND CONCLUSIONS

(1) For the Australian aborigines a simple exponential relationship exists between mean annual rainfall and the size of the tribal territory. For the total series of 409 tribes the equation takes the form of: $Y = 615.00\ X^{-0.98980}$ where Y is the size of the tribal territory and X is the mean annual rainfall.

(2) By the systematic exclusion of categories of tribes in which ecological factors change the population density, as compared to an inland terrestrial standard, and by the elimination of tribes in which cultural factors modify the size of the population from the assumed constant of 500 persons, the equation for the basic series becomes: $Y = 7{,}112.8\ X^{-1.58451}$.

(3) The validation of the ecologically and culturally excluded tribal categories through the area ratio method yields preliminary data toward the establishment of a quantitative human ecology in Australia. Densities are

increased measurably by the marine foods available to coastal and insular tribes. Riverine foods from unearned surface water may provide the greatest increase in density. Among the cultural factors, advanced political organization may result in a marked increase in the size of the tribal population, whereas the recent acquisition of either or both circumcision and subincision ceremonies, for reasons which have not been defined, is associated with a transient decrease in the size of tribal population.

(4) A comparison between the admittedly inaccurate early estimates for the size of tribal populations and estimates based upon the area ratio methodology confirms the assumption that statistically the size of the Australian tribe approximates 500 persons, with an effective range of variation between 200 and 800. This clustering tendency of tribal population size is apparently based upon territoriality, limited personal mobility, and absence of tribal authority as these factors operate through the forces of social cohesion to define and maintain an effective social entity.

(5) The value of 0.81 for the coefficient of curvilinear correlation of the basic equation results in an explained variance of 65 per cent and an unexplained variance of but 35 per cent. A listing of the categories of errors which have contributed to the unexplained variance indicates that the size of the tribal territory is causally and rigorously determined by the magnitude of the mean annual rainfall. This relationship validates the intervening, independent assumptions that for the basic inland tribes density is an inverse function of the size of the territory and that tribal populations approximate 500 persons in a statistical sense. Thus the basic equation can be rewritten in the form of an equation for density as follows:

$$D = \frac{0.0703037}{X^{-1.58451}}$$

(6) The high degree of correlation between rainfall and density indicates that the Australian aborigines are subject to a rigorous environmental determinism of their densities. There is little reason to believe that most other Recent or Pleistocene hunting and collecting populations were not equally subject to environmental determinism of this nature. An obvious corollary is that such populations were in equilibrium with their environment, provided that culture, and hence extractive efficiency, was but slowly changing.

(7) The methodology here developed for Australia can be extended to simple hunting and collecting populations at other points of time or space, but the density equation will differ in terms of: (a) the variables of the environment critical for the biota; (b) the variables of the phylogenetic history of the local biota; and (c) the variables of culture which determine the extractive efficiency of a population.

(8) Applications of this study for Australia allow the correction of existing tribal maps to approximate an idealized distribution of genetic isolates for use in gene flow models. Similar genetic grids can be constructed for various points in prehistory when paleoclimatological estimates for mean annual rainfall in times past become available. Such instruments will al-

low the taking of prehistoric censuses and the determination of the pattern of distribution of prehistoric densities, even extending out onto the now submerged Sahul Shelf.

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